ECOLOGICAL MONOGRAPHS

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ECOLOGICAL MONOGRAPHS

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FOR ALL PHASES OF BIOLOGY

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PHYTOSOCIOLOGY OF THE NASH CRATER LAVA FLOWS, LINN COUNTY, OREGON

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INTRODUCTION

The central and upper montane region of the Cascade mountains of Oregon, the Santiam-McKenzie area, is mantled by a series of forest communities each quite different in structure, complements of species, and syngenetic history. These are coniferous associations which vary from a few protected primeval remnants and noneconomic primary subclimaxes to vast lumbered and burned forests in various stages of secondary succession. At mid-altitudes, the normal belted-mosaic of their orographic continuity is altered, regardless of degree of disturbance, because a superimposition of the Pleistocene High Cascade mountain range upon the eastern flank of the Miocene Western Cascade range created a large, central trough or valley and thus a slight rainshadow. The more mesic species of the upper montane forest, which are found on the eastern slope of the Western Cascades, are excluded.

The upper montane forest is further altered edaphically because of a sporadic vulcanism of the present millennium. Viscid basaltic magmas poured out of parasitic vents along the western slope of the High Cascades and flowed west to the bottom of the above-mentioned trough or Western-High Cascade junction (designated the McKenzie trough in the study area). Subsequently, the end stages of this interim were marked by mild explosions of ejecta which built up symmetric, presently undissected, scoria and lapilli cones. Also, extensive ash and lapilli mantles were deposited to the lee of the craters by the prevailing northwest winds. Thus dense climax forest which extends down over weathered lavas, tuffs, and glacial tills from the crest of the Western Cascades gives way sharply to thin developmental stands which are scattered out over the lavas and sterile ash flats.

The Santiam or northern portion of the McKenzie trough was chosen for study of this difference in forest communities. The area lies in the northeast part of the Willamette National Forest and in the east central portion of Linn County, Oregon. The

flows cover an area of approximately ten square miles the coordinates of which are 44° 28′ north latitude and 121° 59′ west longitude (Fig. 1). Their western boundaries are marked by two intermittent lakes, Fish and Lava Lakes, which are 3200 feet in elevation. The eastern boundary of the flows is just beyond their point of origin where the ash flats to the lee of Nash Crater overlap with the deposits of the higher craters at 4200 feet elevation. Their southern limits, continuous with the crater chain to the south, were arbitrarily placed at Sand Hill road.
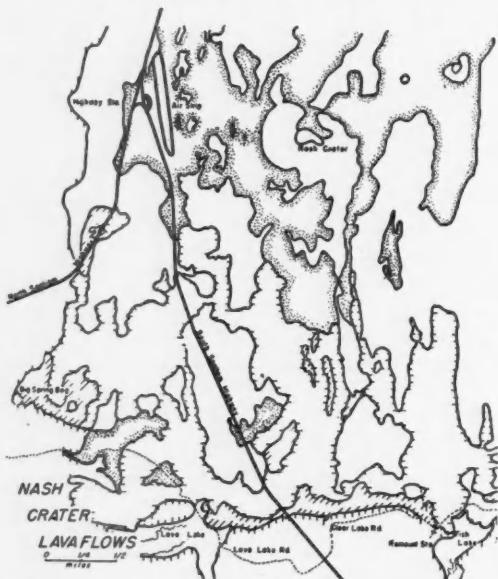
FIG. 1. A map of the distribution of the associations of the Nash Crater lava flows. The different borders represent the following associations: dotted—*Pinetum contorti lapillosum;* clear—*Pseudotsugeto-abietum grandis;* horizontal lines—*Pseudotsugeto-abietum lasiocarpae;* oblique lines—*Aceretum circinati lavosum;* vertical lines —*Pseudotsugetum taxifolia tsugosum.*

To the north, the lavas of Little Nash terminate on an east-west line just beyond Fish Lake.

The purpose of this present paper is: (1) to designate the developmental communities on the lavas; (2) to enumerate the floristics of each; *i.e.* to show the quantitative, qualitative, and synthetic phytosociologic values which fix and define a community as to its structure, its variation within its extent, and its progressive stages of development to a stable terminus; (3) to classify these communities on a basis of the present composition of each; and (4) to attempt to explain sociologic variation and difference through an interpretation of the environmental controls. Also, these floristics are compared with those of the climax forest which borders the periphery of the flows.

Finally, since phytosociological studies in the Pacific Northwest are few, it is hoped that the floristic studies of this paper may serve as a focal point for a future recognition and eventual classification of the associations of two possible alliances. These may be the western and eastern *Pseudotsugiones* of the coniferous order of western North America since the montane associations of the Pacific Northwest are probably affiliated by the presence of Douglas fir *(Pseudotsuga taxifolia)* in their association lists, and likewise many of the forest aggregations of the Rocky Mountain chain, though varying floristically from those of the west, are united through the presence of Douglas fir.

GEOLOGY

EARLY VOLCANIC HISTORY

The geology of the Cascadian chain, and subsequent topography and climatic differentiation, is the ultimate *raison d'etre* for the present macro-aspection of mid-Cascadian forest types. This chain is composed of a vast composite of magmatic products ejected in many different ways for an almost continuous activity during the past 60 million years. Its history has been compiled from many sources and simply accounted by Williams (1948). Hence, the following generalization of the early continuity is taken largely from his narrative.

The Larimide revolution, which created the vast Rocky Mountain folded anticline at the end of the Cretaceous Period, was a far-reaching series of crustal movements which uplifted the western portion of the continent. These upheavals ushered in the prelude of far-western eruptions along an extensive north-south fault line.

In middle and late Eocene, a few volcanoes began the rudiment of the Cascade belt. These scattered ancestral cones continued to increase their outpourings, and by the middle Oligocene their products of ashes, agglomerates, andesitic and basaltic lavas

were piled up to depths as great as 10,000 feet. However, up to the great consolidation period of the middle Miocene, these were coastal mountains, and it was a period of rhythmic subsidence or settling of these aggradations.

At the end of the Miocene, folding and tilting earth movements lifted the Cascades *en masse*. The most significant effect of the uplift was an opening of a band of fissures along the eastern flank and near the crest of this single range. From these new vents and during the following Pliocene, a second range evolved, the High Cascades which was composed of large shield volcanoes.

The Western Cascades were built from quiet effusive flows, while the High Cascades in their final stages of growth became explosive. Parasitic cinder cones developed on the flanks of the shields which buried them with ejecta, and this consolidation continued into the Pleistocene.

In addition, during this period, the high range was mantled with thick mountain glaciers which at times reached out 20 miles or more and attained depths of more than 1000 feet. Thayer (1939) recognized three stages of glaciation in the Santiam region. These are the Mill City, Detroit, and Tunnel Creek. He correlated them with the Sherwin, Tahoe, and Tioga glacial stages of the Sierra Nevada which in turn correspond to the Kansan, Iowan, and Wisconsin continental glacial epochs respectively (Blackwelder 1931). Moreover, Thayer found that the McKenzie trough was filled with ice during the first two stages, and that the ice mass was comprised of two glaciers, one moving north and the other south from the north-south Fish Lake divide in the study area.

THE NASH CRATER LAVAS

During the 25,000 years following the retreat of ice from the mid-Cascadian trough, vulcanism diminished, though a few sporadic eruptions occurred at intervals throughout the chain. Of this minor activity, Williams (1944) mentioned the many small cones of the Santiam-McKenzie area as the most recent because of the presence of a forest on the bottom of Clear Lake (five miles south of Fish Lake). The forest was covered when the McKenzie River was cut off by the lavas.

Apparently the line of cones in this region, along the western flank of the old shield volcanoes, represents a series of parasitic vents from which first poured viscid black basalts that flowed west to the lowest part of the McKenzie trough. Then in the waning stages, underground differentiation took place and explosive ejecta were blown out to form small cinder cones of scoria and lapilli.

Nash and Little Nash Craters are at the north end of this chain. Nash Crater, the larger of the two, stands as a symmetric cone 770 feet above its ash-covered base, and has a crescent-shaped crater which is 100 feet in depth. Little Nash is 300 feet in height and its crater is at base-level. Because of the prevailing northwest winds, the eastern rims of

both craters were built of wind-borne lapilli 200 to 300 feet higher than their western rims. The finer ash was deposited in deep mantles to the lees of both cones.

Overall cone structure was shown in sequences of ejecta from Little Nash Crater which were graphically marked in highway cuts. A profile from the lee base was indicative of the composition of the ash and lapilli flats to the south-east in which one foot of ash covered 46 feet of coarse yellow lapilli. One 12-foot profile of alternate layers of sorted scoria were indicative of the cascades which built the cone. A profile of an old moraine 100 feet from its northeast base showed that two feet of ash overlie six feet of black volcanic sand; beneath were three small strata of progressively larger scoria; a thin layer of white fragmentary andesite preceded four feet of black ash and volcanic sand; at the 16 to 21-foot levels, yellow ash graded into glacial till; and beneath this deposit, the Pleistocene till, which is composed of reworked gray tuff with interspersed rounded boulders of andesite, lay to a recorded depth of 60 feet.

The basalts which moved west from Nash and Little Nash are apparently of two compositions. One series is a grayer, less angular lava in which finer volcanic detritus is intermixed. Being scoriaceous, it was originally very hot lava. Further away from the cones at lower elevations and at the outermost extensions, the second series of basalts is dark, less scoriaceous, and thus was relatively cooler. Those latter flows are loosely broken up into a jumble of sharp-edge blocks with large substral interstices. Undoubtedly these lavas had a high viscosity and moved slowly since no evidences of ropy or obsidian lavas were found. And in addition, the gradient of flow of both series was rather steep, and the succession of waves with steep faces form a progression of benches.

That this vulcanism is recent is attested by the presence of the drowned forest in Clear Lake, the lack of erosion of the soft cones, the presence of ejecta strata on top of glacial till, and by a lack of acquired characters in the substral profiles. Moreover, an exact chronology was suggested by the position of a few Douglas fir, the largest and oldest on the flows, which were found at the western edge of the lavas just south of U. S. Highway 20. The coarse lavas appeared to have been pushed around the trees, and an extensive excavation around one bore out this presumption, for the first lateral roots of the tree lay at six feet below the level of the basalt. Beneath the roots a layer of water-worked gray scoria was interbedded in gray soil. Therefore, one tree was cut down which was symmetric and intact for its age, 85 feet in height, and 68 inches d.b.h.; and a radial wedge was taken for ring analysis.

The stump at three feet above the lava did not display burn scars which might have set the date the tree was surrounded. Yet the skeletal plot of its 638 years showed two major bands of microscopic

rings. For the first nine years it grew rapidly, then its growth gradually tapered off, possibly because of forest consolidation. However, in its 43rd year (595 years ago), it entered a period of restricted growth which lasted for 12 years. It gradually recovered, as was portrayed in its progressively increasing size of rings up to its 178th year (460 years ago). Growth was again restricted severely for 8 years. The remaining 452 rings were complacent.

It is doubtful if these two bands of restricted growth can be ascribed to climatic influence. In the first place, climatic fluctuations do not show in the ring record in areas where optimal temperature and moisture conditions prevail. In the second place, there are 452 years of ring complacency at a time when there was climatic fluctuation as is shown in the tree ring chronologies of lodgepole pine growing on the upland sterile ash flats. Moreover, this particular tree was rooted in soil, and oxygen and water were available through the large interstices of the block lava.

If the above assumptions are true, the two disconformities of growth may be ascribed to some other environmental agency or agencies. It is possible that the first restriction of growth was caused by the basalt flow as it was the first in the chain of volcanic events. The second restriction which occurred 135 years later might represent the most intense period of explosive eruption that built the cones since hot magmatic gases and showers of acid rain could have caused this second series of microscopic rings.

This rough chronology would place the origin of the Nash flows at around 1354 to 1497 A.D. However, it is probable that activity commenced earlier, as the first date represents the terminal or westernmost extention of the basalts. Then during the intervening years cone-building was intermittent, as is evidenced by the series of different ejecta layers from Little Nash Crater; and the latter date may not represent the terminus of this activity, but merely its most intense period.

MACRO-CLIMATE

Though Oregon's latitudinal position is at the southern border of the wet microthermal, boreal province, its land-mass to ocean-mass relation, together with the prevailing movements of the Polar Pacific air mass from the northwest, furnishes it with a distinct mesothermal, maritime climate. This air mass is cold, humid, and unstable but warmer than the land over which it passes in the wintertime. As a result, the cooling effect of the land and of a shore-continental upwelling, together with the relative instability of the air mass, produces heavy winter precipitation. To the south, the Tropical Pacific air mass acquires a warm, humid, and unstable character from the ocean over which it lies. It is pulled north by the movement of the westerlies, overriding the colder Polar Pacific air and forming warm fronts. In the summer, the land is warmer and the oceans colder, and these movements are reversed. The climate becomes semi-arid.

The preceding pattern is further intensified by the orographic effects of Oregon's land-mass topography. The north-south axes of the Coast and Cascade ranges form effective and almost continuous barriers to the prevailing winter movements of the Pacific air masses. Precipitation-loss is intensified with uplift and cooling as the winds move up and over the range. On the eastern slopes, deprived of their moisture, they descend, compressing, warming up, and taking up moisture. Thus the rest of Oregon east of the Cascades is arid because of this rain-shadow effect.

In addition, the Cascades act as a barrier to the winter movements of the dry, cold and stable Polar Continental air mass. This insures moderate thermal control by the maritime air masses. Occasionally when stagnation is of sufficient duration in the Great Basin, it produces enough pressure to spill cold air over the mountains. The climate becomes continental with low temperatures and snow until major movements within the center of the continent relieves the pressure.

There are few weather stations on the western slopes of the Cascades. Hansen (1947) found that the average mean annual rainfall at seven stations, located from 700 to 3,900 feet, is approximately 91 inches. The precipitation ranges from 62 to 124 inches. He mentions, however, that the temperature data are scanty and not reliable for wide ranges of altitude, and his findings show that roughly there is a difference of about 25° F between maximum and minimum averages.

Ten years of weather records taken on hydrothermographs at the Santiam Junction Highway Maintenance Station, which is within the study area, were analyzed for monthly maximum and minimum variation. Absolute monthly precipitations and their seasonal and yearly variations were typical of a winter-type distribution with peak precipitation during November and December. Figures vary from 16 to 3 inches for this period, and such variance probably depends upon the disposition of the Polar Continental air mass during those years. The dry summer months are shown by low figures for July and August at which time the rainfall may be but a fraction of an inch, and not over 2 inches. This pattern conforms to the earlier described maritime influence. The average annual precipitation is approximately 50 inches.

Variation in maximum and minimum monthly values of temperatures and relative humidities show maritime trends. The former indicate a surprising stability of minimum temperatures around 20° F for the months of May through October. Minimum readings for the winter are relatively moderate and average above 0° F. Correspondingly, the monthly maximum temperatures are evenly high during the summer at between 80 and 100 degrees and become progressively lower to around 50° in February. Through all months there is a greater range between maxima and minima, approximately 50 degrees, than is to be expected for a maritime climatic province. Such a

gap in extremes approaches those found in continental montane climates.

The maximum humidities are high throughout the year differing only slightly from 100 percent. They clearly show that precipitation effectivity is high for some part of each month. The low minimum percents for the summer months are high as in typical maritime summers. However, the high minimum humidities of the winter months indicate a low evaporation potential.

Perhaps the key factor of this region's climate is the cumulative snowfall (U. S. Dept. of Agriculture 1945). As a regulatory body influencing humidity and temperature and controlling the length of the growing season, it distinguishes the mountain maritime type. From October through April the snow pack constantly accumulates and reaches maximum depths as high as 84 inches in February at Santiam Junction. During the last part of April and the first of May, it gradually disappears.

The average depth of this snow pack is 30 inches during the winter. It not only stabilizes extremes of temperature and humidity, but it also acts as an insulator and keeps soil temperatures constant and well above 0° F. During the early part of the growing season in the last week of May and into June, the snow mantle provides a constant supply of both available water and ground storage. Phenologic records show that the major portion of the vegetation completes its life cycles rapidly through June in correspondence with the duration of surface melt water and a limited ground storage.

METHODS

The field work was started in the latter part of May, 1949 and continued through the growing season into the last part of September, 1949. At first, phenologic and taxonomic studies were initiated on prevernal forms, and community-delineation reconnaissances made. Then during the first part of June, sampling areas were laid out in the five distinct developmental associations of the flows and adjoining climax forest. Sampling technique included a location of three widely separated stations or stands in each entity. In each stand nested quadrats were laid out at 100 meter intervals along transects. To simplify and standardize a technique and to cover this number of vegetational units in one season, uniform-sized quadrats were employed as follows (after Oosting 1948): (1) arboreal stratum 100 square meters; (2) frutescent stratum 16 square meters; (3) herbaceous stratum 1 square meter; (4) bryophytic layer ¼ of a square meter. In addition, the following numbers of samples were used as appeared to correctly portray disposition and arrangement of the species and as generally employed and recommended by earlier statistical researches (Billings 1938; Cain 1943; Penfound 1945; Oosting 1948): (1) climax forest, 12 quadrats in each layer; (2) each of the four subclimax communities on the lavas, 50 quadrats in each synusia; (3) three strata of the

bog community, 16 quadrats in each for a total number of 858.

The data from the quadrats at all stations were analyzed for density, percent of density, and frequency. Such values give for the first an index of amount, and for the second, the relationship of such amounts of the species one to another. Space occupied was likewise expressed in relative and percent of total values. For the arborescent species, basal areas were calculated from d.b.h. measurements; for the shrubby and bryophytic species, crown interception was recorded in square meters. Syngenetic data were obtained for the aborescent species by noting the distribution of their total sample numbers throughout the following series of arbitrarily set size (diameter)—classes: reproduction, 1½" to 2½", 3" to 6", 6½" to 12", 12½" to 24", 24½" and over. The remaining floristic analyses embraced phenologic records of the angiosperms, life form designations, and presence lists. All station quantitative, qualitative, and synthetic values were collectively expressed in association tables both as a summary and to save space.

In addition to the preceding floristic data which express the vegetational effect, the following environmental data, which express cause, were obtained. For the edaphic factor group, representative profiles were plotted and soil samples of the layers collected for textural analysis. The portion of each sample retained on a 2 mm screen was noted as a percent of the total. The smaller size classes of the remaining portion were found by using a modified hydrometer method (Bouyoucos 1935). Furthermore, soil pH was determined for the profile strata by colorimetric indicators, and permanent wilting determinations were made. The latter, which can only be regarded as approximately correct or as a relative scale, were secured by multiplying the colloidal percentage of the soil, as obtained hydrometrically, by the constant 0.2835 (Bouyoucos 1930). Also, two micro-climate stations were maintained in shelters at ground level, one in the open block lava and the other in the climax forest. Maximum and minimum temperatures and relative humidities were recorded twice daily at 8 A.M. and 8 P.M. Other environmental influences, such as the biotic and pyric factor groups, were considered through observation and photography.

The community nomenclature followed in this paper is that which has been developed by the European Zurich-Montpellier school (Braun-Blanquet 1932). The unit of classification, or association, is that recommended by the Sixth International Botanical Congress of 1935 which in more recent years, has been further subdivided by several workers into strata or separate floristic units of the whole, the unions (Cain & Penfound 1938; Dansereau 1946; Lippmaa 1939). This taxonomic approach is used in preference to the monoclimax disposition of the Chicagoan and Nebraskan schools, which would apply very well in this area where the successive states of replaceable floras are visible, undisturbed,

and moving toward a stabilized terminus, because of
the objections of Braun-Blanquet (1932) and Con-
ard (1939) who point out (1) that this system lacks
categorical systematization, (2) that many of the
communities are stabilized by their disturbance fac-
tors and never attain the status of their taxa, and
(3) that a theoretical vegetation is a poor basis for
classification once replaced, altered or stabilized.

A collection of the species of this study was placed
in the herbarium of Oregon State College. The
synonymy is principally that of Peck (1941). In
some cases, more recent interpretations by Gilkey
(1947) were substituted. One new species, *Carex
diversistylis* was collected and described (Roach
1952).

COMMUNITY FLORISTICS

THE ASSOCIATIONS AND THEIR DISTRIBUTION

Apparent variability in structure, of species com-
plements, and of environmental affinities seems to
warrant a separation of the vegetation of Nash
Crater lava flows into five associations (Figure 1).
In addition to the Clementsian "visible aspect of
dominance" character of each, they are notably
separated by sharp ecotones.

Around the periphery of the flows, the *Pseudotsu-
getum taxifoliae tsugosum* produces a dense forest
on the glacial tills. It is the upper montane regional
climax dominated by Douglas fir *(Pseudotsuga taxi-
folia)*, western hemlock *(Tsuga heterophylla)*, and
lovely fir *(Abies amabilis)*.

On the flows, the *Aceretum circinati lavosum* is con-
fined to the bare expanses of block basalt. It is
dominated by vine maple *(Acer circinatum)*, and is
most extensively developed around Big Spring Bog
and along the western edge of the lavas.

Three large forest associations each cover approxi-
mately one-third of the area. Restricted to the lower
elevations, the *Pseudotsugeto-abietum lasiocarpae*,
characterized by scattered Douglas fir and alpine fir
(Abies lasiocarpa), prevails on much the same sub-
strate as the *Aceretum circinati lavosum*, though
there are smaller-sized scoria mixed in the broken
crust. The second forest association, the *Pseudot-
sugeto-abietum grandis*, occurs throughout the flows
on the most mesic substrates. These are the grayer,
rounded block basalts in which is mixed a high pro-
portion of volcanic sand and ash, and the scoria
cones—mesic because of their orographic and slope
drainage features. The association is dominated by
Douglas fir and grand fir *(Abies grandis)*.

The third forest association, the *Pinetum contorti
lapillosum*, is confined to the deep ash and lapilli
flats which lie to the lees of Nash and Little Nash
Craters. Scattered stands are also found west of the
craters, north of Lava Lake, and along the highway
and reach to the lip of the crater of Nash Crater up
the lee side where the substrate is one of lapilli
rather than scoria. The arborescent synusia of this
association contains but one species, lodgepole pine
(Pinus contorta var. *murrayana)*.

The fifth association is very small. At the north-
ern-most edge of the area, Little Nash Crater's ba-
salts dammed up an intermittent drainage line. As
a result, a sedge-peat bog formed. Its characteristic
vegetation, dominated equally by *Vaccinium occi-
dentale* and *Carex sitchensis*, is designated as the
Carexeto-vaccinetum occidentalis.

THE *Aceretum circinati lavosum* ASSOCIATION

THE FRUTESCENT SYNUSIA: ACER CIRCINATUM UNION

The structure of this union and the placement of
its components is clearly portrayed in the combined
station phytosociologic data (Table 1). Vine maple,
by virtue of its high percent of frequency (84),
density (3.96), and square meters of cover (25.8),
is perceptibly the controlling dominant of this un-
ion. In addition, its percentage figures of total density
and total cover are 66.7 and 77 respectively. These
data are not absolute but rather are indicative of
interspecific relation. Its closest competitor, cascara
(Rhamnus purshiana), has equivalent percentages of
only 9.1 and 6. The other subdominants of impor-
tance are *Holodiscus glabrescens*, manzanita *(Arcto-
staphylos columbiana)*, and thimbleberry *(Rubus par-
viflorus)*, which have low quantitative values but are
constants of the community as is attested by their
presence in the three stations. The species with low
presence and quantitative values, such as *Spiraea
douglasii* var. *menziesii*, *Amelanchier florida*, and
Sambucus racemosa var. *callicarpa*, co-exist in the
lavas along the shore of Lava Lake.

The scattered aspect of the union denotes the harsh
conditions under which these shrubs survive. The
quantitative growth form of vine maple is low in
comparision to specimens encountered in other asso-
ciations. Likewise, there is a sharp transition of the
union with the climax forest, and an inability of
arborescent species to ecize on the block lava.

THE HERBACEOUS SYNUSIA:
CRYPTOGRAMMO-PENSTEMON UNION

The low number of constants of this union depicts
its poor development (Table 1). The low abundance,
density, and frequence of *Cryptogramma acrosti-
choides*, a small fern, which has the highest com-
bination of quantitative values scarcely enables it to
be called a dominant. It is evenly scattered through-
out the lavas although of low occurrence. *Penstemon
menziesii* var. *davidsonii* and *Juncus parryii* form
clumped mats over pockets of wind-blown ash and
organic debris. The grasses usually grow singly,
barely able to exist, while *Dicentra formosa* and
Trillium ovatum are confined to single stations where
they grow in lava crevices near the ecotone. The
majority of the species listed are encountered in
debris deposited in the lava by high water at Lava
Lake.

THE BRYOPHYTIC SYNUSIA: RHACOMITRIUM PATENS
UNION

One is immediately impressed with the develop-
ment of the moss layer over the block lavas in this
association. The bryophytes reach their maximum
development in this area; however, this development

is by one species, *Rhacomitrium patens* (Table 1). This lithophilous moss rapidly completes its life cycle as the last of the snow melts off in the spring, and it soon curls up and becomes dry as the black basalts warm up.

TABLE 1. Phytosociologic data of the Acer circinatum, Cryptogrammo-penstemon and Rhacomitrium patens unions of the *Aceretum circinati lavosum* association. These are the frutescent, herbaceous, and bryophytic synusiae respectively. Presence, station A—near Big Spring Bog; B—west end of flows near highway; C—Fish Lake. Life form designations are: Ph—phanerophyte; Ch—chamaephyte; H—hemicryptophyte; Cr—cryptophyte; Th—therophyte.

Species	Density Relative	Density % Total	Frequency %	Cover sq. m.	Cover % Total	Life Forms	Presence Stations A	B	C
SHRUBS									
Acer circinatum	3.96	66.7	84	25.8	77	Ph	x	x	x
Rhamnus purshiana	0.54	9.1	50	2.2	6	Ph	x	x	x
Holodiscus glabrescens	0.32	5.4	34	4.3	13	Ph	x	x	x
Arctostaphylos columbiana	0.24	4.4	22	1.0	3	Ph	x	x	x
Rubus parviflorus	0.80	13.3	26	....	..	Ph	-	x	x
Arctostaphylos nevadensis	.04	0.7	4	....	..	Ch	-	x	-
Spiraea douglasii var. menziesii	.02	0.4	2	....	..	Ph	-	-	x
Amelanchier florida	.02	0.4	2	....	..	Ph	-	-	x
Sambucus racemosa var. callicarpa	....	....	..	....	..	Ph	-	-	x
HERBS									
Cryptogramma acrostichoides	0.26	12.2	24	....	..	Cr	x	x	x
Penstemon menziesii var. davidsonii	.16	7.5	18	....	..	Ch	x	x	x
Sedum oregonense	0.22	10.3	16	....	..	Cr	x	x	x
Carex diversistylis	0.22	10.3	16	....	..	Cr	x	x	x
Juncus parryi	0.08	3.7	6	....	..	Cr	x	x	x
Saxifraga integrifolia	0.06	2.8	4	....	..	Cr	x	x	x
Asarum caudatum	0.12	5.6	12	....	..	Cr	x	-	x
Festuca occidentalis	0.04	1.9	2	....	..	H	-	x	x
Trillium ovatum	0.02	.9	2	....	..	Cr	-	x	x
Sitanion hystrix	0.02	.9	2	....	..	H	-	x	x
Stipa thurberiana	....	....	..	....	..	H	-	x	x
Senecio triangularis	0.18	8.6	8	....	..	H	-	-	x
Mertensia paniculata var. borealis	0.22	10.3	4	....	..	H	-	-	x
Dicentra formosa	0.10	4.7	8	....	..	Cr	x	-	-
Smilacina sessilifolia	0.14	6.5	8	....	..	Cr	-	-	x
Stachys ciliata	0.12	5.6	4	....	..	Cr	-	-	x
Arenaria macrophylla	0.10	4.7	8	....	..	Cr	-	-	x
Polemonium carneum	0.04	1.9	2	.	..	Cr	-	-	x
Thalictrum occidentale	0.02	.9	2	....	..	H	-	-	x
Hypericum scouleri	....	....	..	....	..	Cr	-	-	x
Arabis holboellii var. secunda	....	....	..	....	..	H	-	-	x
Smilacina racemosa	....	....	..	....	..	Cr	-	-	x
Radicula curvisiliqua	....	....	..	....	..	H	-	-	x
Rudbeckia occidentalis	....	....	..	....	..	H	-	-	x
Lilium columbianum	....	....	..	....	..	Cr	-	-	x
Apocynum androsaemifolium var. incanum	....	....	..	....	..	Ch	-	-	x
Scrophularia lanceolata	0.02	.9	2	....	..	H	-	-	x
MOSSES									
Rhacomistium patens	....	....	68	3.3	66	H	x	x	x
Rhacomitrium lanuginosum	....	....	12	1.5	30	H	x	x	x
Dicranum scoparium	....	....	24	0.1	2	H	x	x	x
Hypnum fertile	....	....	4	0.1	2	H	-	-	x

INTERRELATIONS OF THE COMMUNITY

The dynamics of this association are but slightly pronounced, as one would expect in such a severe lithosere. Reactions and successions are by necessity processes involving long periods of time. There seems to be a little evidence that a classic series of xerarch stages have occurred or are occurring. The organic erosion of the basalt by crustose lichens followed by foliose lichens and mosses is neither apparent, nor do the herbs seem to depend upon these initial reactions for their establishment. The herbs are found usually in depressions on the blocks which have become filled with wind-blown organic and inorganic material. Likewise, the shrubs are confined to crevices which have accumulated a small measure of soil in the same way. The greater consolidation of both the shrub and herbaceous layers nearer the arborescent ecotones is probably accountable to a greater filling-in by organic matter from the forest. Also, several occurrences of tree seedlings were found in the herbaceous mats, but these dry out early in the growing season.

The frequency plots of the unions, attest the youthfulness of the association and its lack of consolidation (Fig. 2). In particular, the paucity of the herbaceous layer is shown by the high percent of species in class A with no percentages of species in the higher classes. Sometimes this variation from the "normal" is indicative of the primary stages of secondary subseral succession. However, in this case, the severity of environment has produced a relative stability and it is within the amplitude of only a few plants to inhabit the basalts.
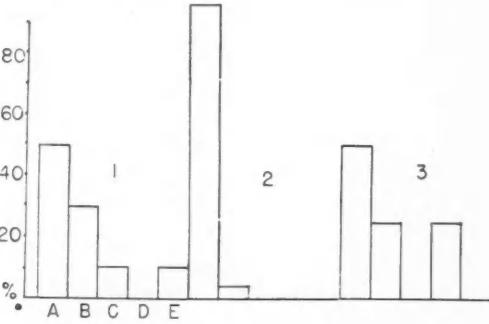
FIG. 2. Frequency graphs of the unions of the *Aceretum circinati lavosum*. 1—frutescent; 2—herbaceous; 3—bryophytic. The capital letters represent the percentage of species (y-axis) that had the following frequencies: A-0 to 20%; B-21 to 40%; C-41 to 60%; D-61 to 80%; E-81 to 100%.

A lack of stratification and consolidation is also shown in Fig. 2. There is, then, little or no interaction or specific dependence between layers. The social or community interactions are loosely knit, and the species as pioneers are dependent upon their own individual amplitudes to occupy the area. Such

organization is an extreme of non-co-ordination when compared to the stratification and sciophytic dependence of the lower unions of a climax forest.

Aspection of the frutescent stratum is divided into two phases. The dominant, vine maple, and manzanita are vernal species (Table 2); whereas, *Holodiscus glabrescens* and thimbleberry are distinctly estival. Most of the forbs and grasses on the lavas proper are prevernal and vernal. *Penstemon menziesii* var. *davidsonii* and *Juncus parryii* are quite early and *Saxifraga integrifolia* completes its life cycle in less time than other flowering plants in the area. One other of the more important herbs, *Sedum oregonense*, predominates in the barren summer aspect.

TABLE 2. Phenology of the shrubs and herbs of the *Aceretum circinati lavosum* association for the growing season of 1949 from the middle of May to the last of September.

Species	Months				
	May	June	July	Aug.	Sept.
SHRUBS					
Acer circinatum	- - - x	x ‡ ‡ ‡	0 0 0 0	0 0 0 0	0 - -
Rhamnus purshiana	- - - -	- † x ‡	‡ ‡ 0 0	0 0 0 0	? ? ?
Holodiscus glabrescens	- - - -	- - - -	- † x x	0 0 0 0	- - -
Arctostaphylos columbiana	- - - x	x ‡ ‡ ‡	0 0 0 0	0 0 0 0	0 0 0
Rubus parviflorus	- - - -	- - - x	x ‡ ‡ 0	0 0 0 -	- - -
Arctostaphylos nevadensis	- - - x	x x ‡ ‡	‡ 0 0 0	0 0 0 0	0 0 0
Spiraea douglasii var. menziesii	- - - -	- - - -	† † † x	x x ‡ ‡	0 0 0
Amelanchier florida	- - - x	x x x x	x ‡ ‡ 0	0 0 0 0	0 0 -
Sambucus racemosa var. callicarpa	- - - x	x x ‡ ‡	0 0 0 0	0 0 0 0	0 0 0
HERBS					
Penstemon menziesii var. davidsonii	- - - x	x x ‡ ‡	‡ 0 0 0	0 0 0 0	0 0 0
Sedum oregonense	- - - -	- - † x	x x x x	‡ ‡ 0 0	- - -
Carex diversistylis	- - - x	x x 0 0	0 - - -	- - - -	- - -
Juncus parryii	- - - x	x x 0 0	0 - - -	- - - -	- - -
Saxifraga integrifolia	- - - x	x ‡ 0 0	0 - - -	- - - -	- - -
Asarum caudatum	- - - -	x x x 0	0 0 0 0	0 - - -	- - -
Festuca occidentalis	- - - -	- x x 0	0 0 0 0	- - - -	- - -
Trillium ovatum	- - - -	x x ‡ ‡	‡ 0 0 0	0 - - -	- - -
Sitanion hystrix	- - - -	- x x 0	0 0 - -	- - - -	- - -
Stipa thurberiana	- - - -	- x x 0	0 0 0 0	0 0 - -	- - -
Senecio triangularis	- - - -	- - - -	- - - x	x x x ‡	‡ 0 0
Mertensia paniculata var. borealis	- - - -	- - - -	- - x x	‡ ‡ ‡ 0	0 0 0
Dicentra formosa	- - - -	- - - x	x ‡ ‡ 0	0 - - -	- - -
Smilacina sessilifolia	- - - -	- x x x	‡ ‡ ‡ 0	0 0 - -	- - -
Stachys ciliata	- - - -	- - - x	x ‡ ‡ 0	0 0 - -	- - -
Arenaria macrophylla	- - - -	x x x ‡	‡ ‡ 0 0	0 0 - -	- - -
Polemonium carneum	- - - -	- - - †	x x x ‡	‡ x x ‡	‡ ‡ 0
Thalictrum occidentalis	- - - -	- - - x	x ‡ 0 0	0 0 - -	- - -
Hypericum scouleri	- - - -	- - - -	- - - -	x x x ‡	‡ ‡ 0
Arabis holboellii var. secunda	- - - -	x ‡ ‡ ‡	‡ ‡ ‡ 0	0 0 - -	- - -
Smilacina racemosa	- - - -	x x x ‡	‡ 0 0 0	0 0 - -	- - -
Radicula curvisiliqua	- - - -	- - - x	‡ ‡ ‡ ‡	‡ ‡ ‡ ‡	‡ ‡ 0
Rudbeckia occidentalis	- - - -	- - - -	- - x x	x ‡ ‡ ‡	‡ ‡ 0
Lilium columbianum	- - - -	- - - -	- - - x	‡ 0 0 0	- - -
Apocynum androsaemifolium var. incanum	- - - -	- - - -	- - † x	‡ ‡ 0 0	0 ? ?
Scrophularia lanceolata	- - - -	- - - -	x ‡ ‡ ‡	‡ ‡ 0 0	0 - -

- - floral inactivity; † - in bud; x - flowering; ‡ - flowering and fruiting; 0 - fruiting; ? - unknown.

THE PSEUDOTSUGETO-ABIETUM LASIOCARPAE ASSOCIATION

THE ARBORESCENT SYNUSIA: PSEUDOTSUGETO-ABIES UNION

The constants of this union, found at all three stations, are two species, Douglas fir and alpine fir (Table 3). That the union is poor in species is not surprising in that the conditions for growth and establishment are not much different from those of the *Aceretum circinati lavosum*.

Both Douglas fir and subalpine fir control this stratum and the association. Their low densities and high frequencies depict an open forest in the first stages of consolidation (Fig. 3). Douglas fir has a high relative basal area which for 53 trees totals 32,006 square inches and is 96 percent of the basal areas of all species. On the other hand, alpine fir

TABLE 3. Phytosociologic data of the Pseudotsugeto-abies, Acer circinatum, Sedum oregonense, and Rhacomitrium patens unions of the *Pseudotsugeto-abietum lasiocarpae* association. These are the arborescent, frutescent, herbaceous, and bryophytic synusiae respectively. Presence, stations A—Lava Lake; B—highway at the west end of flows; C—south of Nash Crater. Life form designations as in Table 1.

Species	Quantitative					Quali-tative	Syn-thetic
	Density		Frequency %	Space		Life Forms	Presence Stations A B C
	Relative	% Total		Basal Area sq. in.	% Total		
TREES							
Pseudotsuga taxifolia	1.06	44.0	88	32,006	96	Ph	x x x
Abies lasiocarpa	1.28	54.0	76	1,238	4	Ph	x x x
Tsuga heterophylla	0.02	0.8	2	50	0	Ph	- x -
Pinus contorta var. murrayana	0.02	0.8	2	3	0	Ph	- - x
Tsuga mertensiana	....	....	..	....	..	Ph	- x -
Abies grandis	....	....	..	....	..	Ph	- - x
SHRUBS				Cover (sq.m.)			
Acer circinatum	1.06	17.1	78	17.7	56	Ph	x x x
Arctostaphylos nevadensis	4.40	45.0	36	3.5	11	Ch	x x x
Castanopsis chrysophylla	0.68	7.0	34	4.8	15	Ph	x x x
Pachistima myrsinites	1.20	12.3	12	1.5	5	Ph	x x x
Rhamnus purshiana	0.50	5.1	32	1.1	3	Ph	x x x
Holodiscus glabrescens	0.50	5.1	18	1.1	3	Ph	x x x
Arctostaphylos columbiana	0.20	2.0	14	1.1	3	Ph	x x x
Rubus parviflorus	0.40	4.1	10	0.2	1	Ph	- x -
Amelanchier florida	0.20	2.0	8	0.4	1	Ph	- - x
HERBS							
Sedum oregonense	0.84	29.4	44	....	..	Cr	x x x
Penstemon menziesii var. davidsonii	0.68	23.8	34	....	..	Ch	x x x
Chimaphila umbellata var. occidentalis	0.68	23.8	24	....	..	Cr	x x x
Carex diversistylis	0.16	5.6	4	....	..	Cr	x x x
Cryptogramma acrostichoides	0.10	3.5	6	....	..	Hr	x x x
Stipa thurberiana	0.10	3.5	6	....	..	H	- x x
Festuca occidentalis	0.20	7.0	10	....	..	H	- x x
Trillium ovatum	0.10	3.5	12	....	..	Cr	x - -
Sitanion hystrix	....	....	..	....	..	H	- x -
MOSSES							
Rhacomitrium patens	....	....	86	3.1	76	H	x x x
Rhacomitrium lanuginosum	....	....	22	0.8	21	H	x x x
Dicranum scoparium	....	....	12	0.1	2	H	x x x

has a basal area of 1,234 inches which is but 4 percent of the total. Since the former occupies so much more space than the latter, it would normally be considered the dominant. However, alpine fir never attains large size, and in this open union, its other quantitative values are both equal to those of Douglas fir and possibly sufficient to extenuate it as a co-dominant (d. 1.28, f. 78). These relationships are supported by the distribution of numbers in the different size-classes (Table 4). Alpine fir ranges through the lower size classes from 1½″ up to 12″ and Douglas fir from 12″ up to 24¼″ and over.

FIG. 3. The structural relationships of the species of the *Pseudotsugeto-abietum lasiocarpae*. Old, large Douglas fir and smaller alpine fir make up the arborescent layer. Scattered vine maple and associated species compose the understory. Note the absence or poor development of the herbaceous union—Photo by C. Heusser (May 1950).

TABLE 4. Size class distribution of the abundance of the arboreal species of the *Pseudotsugeto-abietum lasiocarpae* association.

Species	Repr.	−3	−6	−12	−24	+24	Total
	SIZE (diameter) CLASSES INCHES						
Pseudotsuga taxifolia	8	0	0	5	19	21	53
Abies lasiocarpa	21	8	23	12	0	0	64
Tsuga heterophylla	0	0	0	1	0	0	1
Pinus contorta var. *murrayana*	0	1	0	0	0	0	1
Tsuga mertensiana	..	..	..	..	..	..	..
Abies grandis	..	..	..	..	..	..	..

The former distribution might be interpreted as a greater degree of aggressiveness and thus offset somewhat the cover control of Douglas fir (96 as to 4 t.b.a.).

Lodgepole pine appears in the union at the eastern ecotone of the lodgepole forest with this association. Grand fir and mountain hemlock (*Tsuga mertensiana*) were found outside of the quadrats as small seedlings on duff accumulations in patches of alpine fir.

THE FRUTESCENT SYNUSIA: ACER CIRCINATUM UNION

The ascendancy of vine maple of this stratum is continued over from the adjacent barer basalts

(Table 3). Its qualifications of dominance are an even distribution (f. 75) coupled with sufficient consolidation (d. 1.66) and degree of cover (17.7 sq. m.) which are much higher than those of the other species in the union. *Arctostaphylos nevadensis* (percent t.d. 45.0, f. 36) is much less frequent, though denser, and has only 11 percent of the total cover.

When this union is compared to the frutescent layer of the *Aceretum circinati lavosum*, a high degree of affinity may be shown. The species list is almost identical, except that *Castanopsis chrysophylla* and *Pachystima myrsinites* are able to come in, because of the slight forest influence, from their centers of development in the adjacent Douglas fir-grand fir association. Also, perhaps because of the arborescent layer, the quantitative values of all species are less.

THE HERBACEOUS SYNUSIA: THE SEDUM OREGONENSE UNION

As in the preceding union, forest influence has cut specific quantitative values, and again the species are essentially the same as in the *Aceretum circinati lavosum*. Apparently however, as in the frutescent stratum, the arborescent layer has not conditioned the environment sufficiently to permit a more mesic complement to become established.

Sedum oregonense, though quantitatively the highest of the species, has values (d. 0.84, f. .44) which are not high enough for it to suffice as a spatial or "controlling dominant" according to the monoclimax dictum (Table 3). Several species found in the vine maple association have dropped out, and many of the remaining have high presence. Thus the layer is scattered, but constant, and poorly developed. One species, *Chimaphila umbellata* var. *occidentalis*, has moved in slightly and with high presence from the *Pseudotsugeto-abietum grandis* association.

THE BRYOPHYTIC SYNUSIA: RACOMITRIUM PATENS UNION

Table 3 shows that there is but little variation in this union from that of the open lavas. As a matter of fact, the species complement is identical and the interspecific relations are the same. *Rhacomitrium patens* has little or no quantitative variation, nor does the slight environmental change affect either its absolute or its relative dominance over the other species.

INTERRELATIONS OF THE COMMUNITY

It has already been noted that this is a transitional community. Its individuality lies in the consolidation of alpine fir and the restriction of this species to this aggregation; moreover, the lower strata are transcended from the *Aceretum circinati lavosum* so that it is the vine maple association, except for a few minor changes, with an arborescent stratum. Dynamically, it is the second in a syngenetical sequence which will be developed in the integration portion of this paper. Internally, the scattered composition, the high presence of the frutescent layer, and the slight infiltration of mesic species point to a very

slow or long term replacement. In the irregular frequency plots, the class D and E percentages of the arborescent graph denote a stable community; whereas, the B and C class gaps are indicative of a poor species complement (Fig. 4). The graphs of the next two strata are superficially similar to floras undergoing rapid exchange, extinction, and establishment of stable, ultimate dominants. The phytographs of the combined quantitative data of the tree layer show that all species but the "co-dominants" are ephemeral and show no tendencies towards expanding in this community (Fig. 5). The radii of the Douglas fir diagram denote it as an ultimate aggressor and those of the alpine fir diagram superficially show a species which has come in after Douglas fir and is rapidly extending itself because of high density, frequency, and most of the lower size classes since its basal area is low. Thus ultimately it would consolidate, reach the larger size classes and become a "sub-climax dominant." However, the data of Table 4 show that the missing size classes of Douglas fir are the lower and those of alpine fir the

FIG. 4. Frequency diagrams of the synusiae of the *Pseudotsugeto-abietum lasiocarpae* association. 1—arborescent; 2—frutescent; 3—herbaceous; 4—bryophytic; otherwise legend same as for Fig. 2.

FIG. 5. Phytographs of the arborescent species of the *Pseudotsugeto-abietum lasiocarpae* association. The top radius of the circle represents percent of total density; the right hand radius represents percent frequency; the lower radius represents number of size classes occupied; the left hand radius represents the percent of the total basal area.

higher and because of the genetic nature of alpine fir it is doubtful if the basal area relationships of the two species would change.

Phenologic cycles are identical to those of the same species in the vine maple association. And as in the preceding association, social affinities are neither clear cut nor very binding, since as the quantitative data have shown, little or no vertical zonation is present.

THE PSEUDOTSUGETO-ABIETUM GRANDIS ASSOCIATION

THE ARBORESCENT SYNUSIA: PSEUDOTSUGETO-ABIES UNION

This is the most varied, syngenetically and socially advanced arborescent layer of the developmental communities. Its species complement is the richest, and its consolidation relatively high (Table 5). The pattern of species disposition is quite pronounced. This mosaic is comparable to a number of facies in an associes. The union is tied together and dominated by Douglas fir. This species has 45 percent of the total density of the 12 species, a density of 7.2, a frequency of 100 percent, and 78 percent of the total basal area.

The forest is developed on the gray basalts which have a high amount of finer ejecta mixed in. Along the South Santiam Highway and from Sawyer's Cave to the foot of Nash Crater, the union is almost pure Douglas fir. On the mesic higher benches north of Nash Crater and on its slopes, grand fir is vigorous and occupies as much or more of the canopy. In this portion of the association lodgepole pine enters along the transition into the ash flats.

Orographic effect and drainage provide Nash Crater's scoria slopes with the most favorable substrate on the flows. In addition to grand fir and Douglas fir, there are present climax elements such as lovely fir, white pine *(Pinus monticola)*, and western hemlock. At the top of the crater, the inner northwest-facing slope has a few individuals of subalpine distribution. These are mountain hemlock and Engelmann spruce *(Picea engelmanni)*. On the mesic northwest-facing slope of the cone, the stratum is predominately grand fir; and on the xeric southeast-facing slope, it is composed of lodgepole pine, western yellow pine *(Pinus ponderosa)*, and Douglas fir. In addition to Douglas fir, only grand fir has sufficient presence to rank as a type species of the association. Quantitatively, (percent t.d. 25.6; f. 72; percent t.c. 11) it does not meet the qualifications for co-dominance because of its low basal area. However, its distribution of abundance in the lower of the range of size classes indicates its active consolidation (Table 6). The data of this table also show a high abundance of Douglas fir in the lower size classes (R-81, 1-54, 2-95, 3-54, 4-55, 5-13) and a uniform spread in the others. This distribution is unusual for the species and this is the only association in which it achieves optimal, progressive increase. The remaining species have low presence and are infiltrants or records from ecotonal quadrats.

TABLE 5. Phytosociologic data of the Pseudotsugeto-abies, Castanopsis chrysophylla, Chimaphila umbellata, and Rhacomitrium patens unions of the *Pseudotsugeto-abietum grandis* association. These are the arborescent, frutescent, herbaceous, and bryophytic synusiae respectively. Presence, stations A—South Santiam Highway; B—Nash Crater; C—Fish Lake. Life form designations as in Table 1.

Species	Quantitative					Quali-tative	Syn-thetic
	Density		Frequency %	Space		Life Forms	Presence Stations A B C
	Relative	% Total		Basal Area sq. in.	% Total		
TREES							
Pseudotsuga taxifolia	7.24	45.3	100	30,666	78	Ph	x x x
Abies grandis	4.10	25.6	72	4,352	11	Ph	x x x
Pinus contorta var. murrayana	2.44	15.0	36	1,409	3	Ph	x x -
Pinus monticola	1.30	8.2	32	1,892	5	Ph	- x -
Tsuga mertensiana	0.24	1.5	4	317	1	Ph	- x -
Pinus ponderosa	0.04	0.2	2	397	1	Ph	- x -
Abies amabilis	0.16	1.0	8	198	0	Ph	- x -
Abies lasiocarpa	0.34	2.1	22	39	0	Ph	- x -
Tsuga heterophylla	0.10	0.6	8	3	0	Ph	- x -
Picea engelmanni	0.04	0.2	4	3	0	Ph	- x -
Abies concolor	....	....	..	...	..	Ph	- - x
Populus trichocarpa	....	....	..	...	..	Ph	- - x
SHRUBS				Cover (sq.m.)			
Castanopsis chrysophylla	3.70	23.7	84	29.0	60	Ph	x x x
Pachistima myrsinites	4.80	30.7	42	5.7	12	Ph	x x x
Acer circinatum	1.36	8.7	10	4.3	8	Ph	- x -
Rubus parviflorus	2.44	15.6	36	2.9	6	Ph	- x -
Ceanothus velutinus	0.76	4.9	26	3.0	6	Ph	- x -
Salix sp.	0.34	2.2	26	1.1	2	Ph	- x -
Rhamnus purshiana	0.42	2.7	24	0.8	2	Ph	x - -
Berberis nervosa	0.50	3.2	14	0.8	2	Ch	- x -
Vaccinium membranaceum	0.40	2.5	8	0.3	0	Ph	- x -
Rubus vitifolius	0.58	3.7	10	0.3	0	Ch	- x -
Arctostaphylos nevadensis	0.28	1.8	8	0.1	0	Ch	x - x
Rosa gymnocarpa	0.02	0.1	2	0.0	0	Ph	- x -
Helodiscus glabrescens	0.02	0.1	2	0.0	0	Ph	x - -
Arctostaphylos columbiana	....	....	..	...	..	Ph	x - -
Vaccinium myrtillus var. microphyllum	....	....	..	...	..	Ch	- x -
HERBS							
Chimaphila umbellata var. occidentalis	1.86	20.8	44	...	..	Cr	x x x
Linnaea borealis var. americana	1.10	12.3	22	...	..	Ch	x x x
Festuca occidentalis	0.12	1.3	8	...	..	H	x x x
Xerophyllum tenax	0.12	1.3	4	...	..	H	x x x
Penstemon cardwellii	0.56	6.3	8	...	..	Cr	x x -
Carex diversistylis	0.30	3.4	8	...	..	Cr	x - x
Sedum oregonense	0.00	0.0	3	...	..	Cr	x x -
Penstemon menziesii var. davidsonii	0.12	1.4	6	...	..	Ch	x - x
Hieracium albiflorum	0.86	9.6	34	...	..	H	- x -
Fragaria bracteata	0.54	6.1	32	...	..	H	- x -
Anemone deltoidea	0.54	6.1	14	...	..	H	- x -
Achlys triphylla	0.30	3.3	10	...	..	H	- x -
Arenaria macrophylla	0.24	2.7	8	...	..	Cr	- x -
Penstemon confertus var. procerus	0.54	6.1	10	...	..	Cr	- x -
Clintonia uniflora	0.54	6.1	14	...	..	Cr	- x -
Smilacina sessilifolia	0.30	3.4	32	...	..	Cr	- x -
Cornus canadensis	0.04	0.4	2	...	..	Cr	- x -
Lilium washingtonium	0.12	1.3	4	...	..	Cr	- x -
Carex inops	0.02	0.2	2	...	..	Cr	- x -
Galium triflorum	0.02	0.2	2	...	..	H	- x -
Pteridium aquilinum var. pubescens	0.10	1.1	6	...	..	Cr	x - -
Eriogonum nudum	0.12	1.4	10	...	..	H	- x -
Trillium ovatum	0.10	1.1	6	...	..	Cr	- x -
Hieracium greenii	0.04	0.4	2	...	..	Ch	x - -
Phacelia californica	0.04	0.4	2	...	..	H	- x -
Pyrola picta	0.12	1.4	6	...	..	Cr	- x -
Listera convallarioides	0.06	0.6	6	...	..	H	- x -
Pyrola secunda	0.06	0.6	2	...	..	Cr	- x -
Lathyrus bijugatus var. sandbergii	....	....	..	...	..	H	x - -
Pyrola bracteata	....	....	..	...	..	Cr	- x -
Antennaria racemosa	....	....	..	...	..	Cr	- x -
Chimaphila menziesii	....	....	..	...	..	Cr	- x -
Juncus parryii	....	....	..	...	..	Cr	x - -
Goodyera decipiens	....	....	..	...	..	Cr	- x -
Apocynum androsaemifolium var. incanum	....	....	..	...	..	Ch	x - -
Bromus vulgaris var. eximius	....	....	..	...	..	H	x - -
Trisetum spicatum	....	....	..	...	..	H	x - -
Polystichum lonchitis	....	....	..	...	..	Cr	- x -
Polypodium hesperium	....	....	..	...	..	Cr	x - -
Woodsia scopulina	....	....	..	...	..	Cr	x - -
MOSSES							
Rhacomitrium patens			42	4.1	45	H	x x x
Rhacomitrium lanuginosum			4	0.8	8	H	x x x
Hypnum fertile			8	0.2	2	H	- x -
Dicranum scoparium			22	0.05	1	H	- x x
Aulacomnium androgynum			4	0.05	1	H	x - x
Rhytidiadelphus triquetrus			4	2.0	22	H	- x -
Polytrichum juniperinum			7	0.9	10	H	- x -
Bryum minictum			3	0.7	7	H	x - -
Ditrichum sp.			3	0.3	3	H	x - -
Leptobryum pyriforme				...	..	H	x - -
Homalothecium nuttallii				...	..	H	x - -

TABLE 6. Size class distribution of the abundance of the arboreal species of the *Pseudotsugeto-abietum grandis* association.

Species	Size (diameter) Classes—Inches						
	Repr.	−3	−6	−12	−24	+24	Total
Pseudotsuga taxifolia	81	54	95	54	55	13	362
Abies grandis	86	32	59	17	11	0	205
Pinus contorta var. murrayana	26	81	13	9	3	0	122
Pinus monticola	21	6	22	15	2	0	66
Tsuga mertensiana	8	0	1	2	1	0	12
Pinus ponderosa	0	0	0	1	1	0	2
Abies amabilis	4	0	1	3	0	0	8
Abies lasiocarpa	14	1	2	0	0	0	17
Tsuga heterophylla	4	1	0	0	0	0	5
Picea engelmanni	1	1	0	0	0	0	2
Abies concolor	..	..	..	..	..	..	
Populus trichocarpa	..	..	..	..	..	..	

THE FRUTESCENT SYNUSIA: THE CASTANOPSIS CHRYSOPHYLLA UNION

A low number of constants denotes a diversity and heterogeneity of this stratum throughout the association similar to that found in the superior union (presence data, Table 5). It is on the lowland,

drier portions of the association that the dominant chinquapin *(Castanopsis chrysophylla)* has its greatest development. Pachistima *(Pachistima myrsinites)* seems qualitatively to be a major feature of the union; but its low growth form (crown cover 5.7 meters) and its greater concentration (abundance 240; frequence 42) under the pure Douglas fir facies relegate it to a sub-dominant role.

The sociological values of the remaining species are negligible. However, certain affinities are apparent. Vine maple and thimbleberry are concentrated on the slopes of Nash Crater. Mesic species of the climax forest, such as *Berberis nervosa, Vaccinium membranaceum, Rubus vitifolius,* and *Rosa gymnocarpa,* also make their appearance at this station. Cinnamon bush *(Ceanothus velutinus)* is encountered in the ecotone where the ash flats and lavas overlap. Moreover, only a few specimens from the preceding two *Acer circinatum* unions are present.

THE HERBACEOUS SYNUSIA: CHIMAPHILA UMBELLATA UNION

The four constants of this union denote the scattered production of the union by their low structural values (Table 5). *Chimaphila umbellata* var. *occidentalis* has a relatively low frequency (44), but a high density (1.9). It is found principally on the lowland lavas with Douglas fir, chinquapin, and pachistima. Twinflower *(Linnaea borealis* var. *americana)* occupies the wetter and shaded sites. *Festuca occidentalis* grows in lava crevices in the shade.

The associated herbs of lesser value can be divided into much the same affinity groupings as were evident in the higher synusiae. Climax forest forbs, such as *Hieracium albiflorum, Anemone deltoidea, Achlys triphylla, Clintonia uniflora,* and others, are common to the moist slopes of Nash Crater. Likewise, on the open lavas and in the ecotone with the lodgepole association, components of both ash flat and block lava derivation are represented weakly.

THE BRYOPHYTIC SYNUSIA: RHACOMITRIUM PATENS UNION

From its high dominance in the bryophytic union of the vine maple association, *Rhacomitrium patens* has succeedingly lower values in the *Pseudotsugeto-abietum lasiocarpae* to a still lower degree in this association (Table 5). Yet these values, modified by forest influence, are still high, and particularly so in relation to the other species. The center of outgrowth of this union is in the lower areas, since *Rhacomitrium patens* grows only on rock substrate.

A greater number of mosses occurs in this union than in the preceding bryophytic unions or in those to follow. These are mesic mosses which are scattered on the forest floor. Apparently, the degree of consolidation of the upper stratum explains in part their presence in the wetter but darker climax forest no bryophytic stratum exists. *Polytrichum triquestris* grows in the ash-lava ecotone.

INTERRELATIONS OF THE COMMUNITY

Certain groupings of structure in all layers define this association as a heterogenous unit embracing a variety of habitats and associated affinities. However, in each stratum, one or two constants as dominants are sufficient to tie the association together. Also, this association is the highest developmental aggregation, in that there is a slight infiltration of climax forest species, low quantitative and presence values for xeric species, and maximum development of Douglas fir in all size classes. Likewise, the frequency graphs of the herbaceous and bryophytic unions bear out a heterogeneity by the length of the class A columns and an absence of stable species in classes D and E (Fig. 6). The spectra of the frutescent and arborescent layers denote an approximity to climax conditions through the frequencies of their dominants. Yet class B is high in both and either C
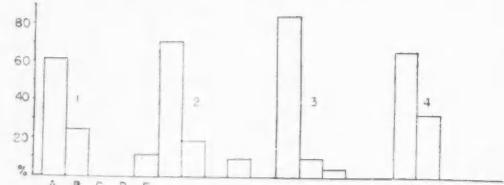
FIG. 6. Frequencies of the synusiae of the *Pseudotsugeto-abietum grandis* association. Graph legend the same as for Fig. 4.

or D is missing, an index of incomplete stability. The phytographs show that all species except Douglas fir are restricted or adventive (Fig. 7). Complete control is shown by the diagram for Douglas fir. The radii for grand fir show it to be a young species which is aggressive and increasing since its one size class is one of the larger as indicated by low percentage of total basal area and it has fair density and frequency. Undoubtedly it will become a co-dominant in time.

The phenologic record of the flowering plants is not as well defined into aspects as in the preceding communities. Perhaps again this is a result of the habitat variety. As a general rule the mesic species are estival on their higher and cooler sites (Table 7). Prevernal species from the previous communities are slightly later, presumably because of the greater duration of the snow pack under the forest cover. Both dominants, chinquapin and *Chimaphila umbellata* var. *occidentalis* of the shrub and herb layers, respectively, are estival. Also of note is the incomplete cycle of a *Salix* sp. This species is able to become established in the forest but the existing conditions are not sufficient for it to have a high degree of vitality.

THE PINETUM CONTORTI LAPILLOSUM ASSOCIATION
THE ARBORESCENT SYNUSIA: PINUS CONTORTA UNION

Striking differences of species complement and structure set this union apart from those of the preceding forest associations which have shown social exchange. Co-extensive with the ash-lapilli mantle to the lee of the craters, lodgepole pine, a species

TABLE 7. Phenology of the shrubs and herbs of the *Pseudotsugeto-abietum grandis* association for the growing season of 1949 from the middle of May to the last of September.

Species	Months				
	May	June	July	Aug.	Sept.
SHRUBS					
Castanopsis chrysophylla	– – –	– – – –	– – – †	x x ‡ ‡	0 0 0
Pachistima myrsinites	– – x	x ‡ ‡ ‡	‡ ‡ ‡ ‡	‡ ‡ + ‡	‡ ‡ ‡
Acer circinatum	– – –	– x ‡ ‡	‡ 0 0 0	0 0 0 0	0 0 0
Rubus parviflorus	– – –	– – – x	x x x ‡	‡ ‡ 0 0	0 – –
Ceanothus velutinus	– – –	– † x x	x x x ‡ 0	0 0 0 0	0 0 0
Salix sp.	– – –	– – – –	– – – –	– – – –	– – –
Rhamnus purshiana	– – –	– – – –	† x ‡ ‡	0 0 0 0	0 ? ?
Berberis nervosa	– – –	† x x ‡	0 0 0 0	0 0 0 0	0 0 0
Vaccinium membranaceum	– – x	x x ‡ ‡	0 0 0 0	0 0 0 –	– – –
Rubus vitifolius	– – –	– – – –	– x x x	‡ ‡ 0 0	0 0 0
Arctostaphylos nevadensis	– – x	x x x ‡	‡ ‡ ‡ 0 0	0 0 0 0	0 0 0
Rosa gymnocarpa	– – –	– – – –	– x x ‡	‡ 0 0 0	0 0 0
Holodiscus glabrescens	– – –	– – – –	– – – †	† x x 0	0 0 0
Arctostaphylos columbiana	– – x	x x ‡ ‡	0 0 0 0	0 0 0 0	0 0 0
Vaccinium myrtillus var. microphyllum	– – –	– – x x	x 0 0 0	0 0 0 0	– – –
HERBS					
Chimaphila umbellata var. occidentalis	– – –	– † † †	† † x x	x ‡ ‡ ‡	0 0 0
Linnaea borealis var. americana	– – –	– – – –	† x x ‡	‡ ‡ 0 0	0 0 0
Festuca occidentalis	– – –	– – – –	– – x x	0 0 0 0	0 0 0
Xerophyllum tenax	– – –	– – – –	‡ ‡ ‡ 0	0 0 0 0	0 0 0
Penstemon cardwellii	– – –	– – – –	– † x x	‡ ‡ ‡ †	0 0 0
Carex diversistylis	– – x	x x 0 0	0 – – –	– – – –	– – –
Sedum oreganense	– – –	– – – –	– † x x	‡ ‡ 0 0	0 – –
Penstemon menziesii var. davidsonii	– – x	x x x ‡	‡ ‡ ‡ ‡	0 0 0 0	– – –
Hieracium albiflorum	– – –	– † x x	x x x x	‡ ‡ ‡ †	‡ 0 0
Fragaria bracteata	– – –	– – x x	x x ‡ ‡	0 0 – –	– – –
Anemone deltoidea	– – –	– † † x	x x x ‡	‡ 0 0 0	0 0 –
Achlys triphylla	– – –	† x x ‡	‡ 0 0 0	0 0 0 0	– – –
Arenaria macrophylla	– – –	– x x x	‡ ‡ ‡ 0	0 0 C ?	? ? ?
Penstemon confertus var. procerus	– – –	– † † x	x ‡ ‡ ‡	‡ 0 0 0	0 0 0
Clintonia uniflora	– – –	– † † x	x ‡ ‡ ‡	‡ 0 0 0	0 0 0
Smilacina sessilifolia	– – –	– – – x	x x ‡ ‡	‡ 0 0 0	0 0 0
Cornus canadensis	– – –	† † x x	x x ‡ ‡	‡ 0 0 0	0 0 0
Lilium washingtonium	– – –	– – – –	– x x x	‡ ‡ 0 0	0 0 –
Carex inops	– – –	– x x 0	0 0 0 0	– – – –	– – –
Gallium triflorum	– – –	– – – –	– x x ‡	‡ ‡ 0 0	0 ? ?
Eriogonum nudum	– – –	– – x x	x x x x	‡ ‡ ‡ 0	0 – –
Trillium ovatum	– – x	x x ‡ ‡	0 0 0 0	0 0 0 0	0 0 0
Hieracium greenii	– – –	– – – –	– x x	x ‡ 0 0	0 0 –
Phacelia californica	– – –	– – x x	x x x ‡	‡ ‡ ‡ 0	0 0 0
Pyrola picata	– – –	– – – –	– † † x	x ‡ 0 0	0 0 –
Listera convallarioides	– – –	– – † x	x x ‡ ‡	‡ 0 0 0	? ? ?
Pyrola bracteata	– – –	– – – –	– – – †	† x x ‡	‡ ‡ ‡
Pyrola secunda	– – –	– – – –	– † x x	x ‡ 0 0	0 0 0
Lathyrus bijugatus var. sandbergii	– – –	– – – –	– x x x	‡ ‡ ‡ 0	0 – –
Antennaria racemosa	– – –	–no record–			
Chimaphila menziesii	– – –	– – – –	† † x x	x ‡ ‡ ‡	0 0 0
Juncus parryii	– – x	x ‡ 0 0	0 – – –	– – – –	– – –
Goodyera decipiens	– – –	– – – –	– † † †	† x x ‡	‡ ‡ 0
Apocynum androsaemifolium var. incanum	– – –	– – – –	– – – –	† x x ?	? ? ?
Bromus vulgaris var. eximus	– – –	– x x 0	0 0 0 0	0 0 0 0	0 – –
Trisetum spicatum	– – –	– x x 0	0 0 0 0	0 – – –	– – –

–floral inactivity; † in bud; x flowering; ‡ flowering and fruiting; 0 fruiting; ? unknown.

TABLE 8. Phytosociologic data of the Pinus contorta, Ceanothus velutinus, Carexeto-penstemon, and Polytrichum juniperinum unions of the *Pinetum contorti lapillosum* association. These are the arborescent, frutescent, herbaceous, and bryophytic synusiae respectively. Presence, stations A—Santiam Junction; B— around and on Nash Crater; C—near the west end of flows near the highway. Life form designations as in Table 1.

Species	Quantitative					Quali-tative	Syn-thetic
	Density		Frequency %	Space		Life Forms	Presence Stations A B C
	Relative	% Total		Basal Area sq. in.	% Total		
TREES							
Pinus contorta var. murrayana	31.25	95.6	100	17,625	86	Ph	x x x
Pseudotsuga taxifolia	0.64	1.9	32	9,969	10	Ph	x x x
Pinus ponderosa	0.18	0.5	14	654	3	Ph	x x –
Abies grandis	0.60	1.8	34	153	1	Ph	– x –
Tsuga mertensiana	0.06	0.2	4	50	1	Ph	– x –
Abies amabilis	0.02	0.0	2	…	0	Ph	– x –
Tsuga heterophylla	0.02	0.0	2	0	0	Ph	– x –
Pinus monticola	….	….	..		..	Ph	– x –
SHRUBS				Cover (sq.m.)			
Ceanothus velutinus	5.96	60.5	66	51.0	75	Ph	x x x
Ribes viscosissimum	0.80	8.1	40	10.0	15	Ph	x x x
Pachistima myrsinites	2.00	20.3	18	3.9	6	Ph	– x x
Arctostaphylos nevadensis	0.68	6.9	26	2.1	3	Ch	– x –
Rubus parviflorus	0.16	1.6	12	0.0	0	Ph	– x –
Juniperus communis var. sibirica	0.16	1.6	6	0.5	1	Ch	– x –
Prunus emarginata	0.06	0.6	2	0.2	0	Ph	– – x
Rhamnus purshiana	0.02	0.2	2	0.0	0	Ph	– x –
Salix sp.	0.02	0.2	2	0.0	0	Ph	– x –
Holodiscus glabrescens	….	….	..		..	Ph	– x –
Castanopsis chrysophylla	….	….	..		..	Ph	– x –
HERBS							
Carex inops	3.20	25.7	52			Cr	x x x
Penstemon confertus var. precerus	5.10	41.0	40	….	..	Cr	x x x
Epilobium angustifolium	0.46	3.7	32	….	..	Th	x x x
Fragaria bracteata	2.22	17.8	34	….	..	H	x x x
Stipa thurberiana	0.20	1.6	14	….	..	H	x x –
Sitanion hystrix	0.18	1.4	10	….	..	H	x x –
Pedicularis racemosa	0.26	2.1	8	….	..	H	– x x
Lomatium angustatum	0.08	0.6	6	….	..	H	x x –
Eriogonum nudum	0.06	0.5	4	….	..	H	x x –
Hieracium greenii	0.06	0.5	4	….	..	H	x x –
Eriogonum mariflorum	….	….	..	….	..	H	x x –
Penstemon menziesii var. davidsonii	0.1	0.8	4	….	..	Ch	– x –
Arenaria macrophylla	0.26	2.1	8	….	..	Cr	x – –
Clintonia uniflora	0.02	0.1	2	….	..	Cr	– x –
Achlys triphylla	0.04	0.3	2	….	..	H	– x –
Haplopappus greenii	0.04	0.3	2	….	..	Ch	x – –
Pyrola secunda	0.02	0.2	2	….	..	Cr	– x –
Spraguea umbellata	0.02	0.2	2	….	..	H	x – –
Lupinus lyallii	0.04	0.3	2	….	..	H	x – –
Pyrola dentata	0.06	0.5	4	….	..	Cr	– x –
Chimaphila umbellata var. occidentalis	….	….		….		Cr	– x –
Sedum oreganense	….	….		….		Cr	– x –
Eriogonum pyrolaefolium var. coryphaeum	….	….		….		Cr	– x –
Anaphalis margaritacea	….	….				Cr	– x –
Arabis holboellii var. secunda	….	….				H	– x –
Aster radulinus	….	….				Cr	x – –
Arabis lyallii	….	….				H	– x –
MOSSES							
Polytrichum juniperinum	….	….	22	2.5	86	H	x x x
Rhacomitrium lanuginosum	….	….	4	0.2	8	H	– – x
Rhacomitrium patens	….	….	4	0.2	6	H	– x x
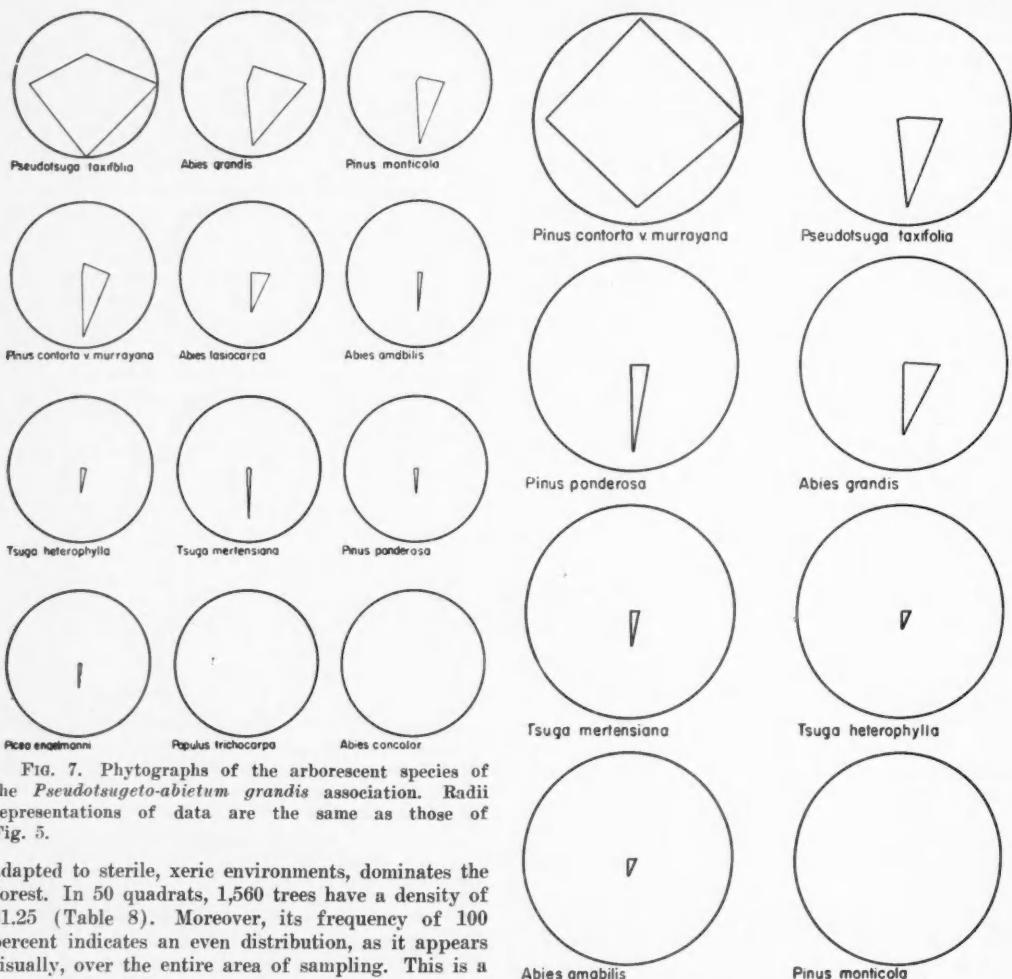
Fig. 7. Phytographs of the arborescent species of the *Pseudotsugeto-abietum grandis* association. Radii representations of data are the same as those of Fig. 5.

adapted to sterile, xeric environments, dominates the forest. In 50 quadrats, 1,560 trees have a density of 31.25 (Table 8). Moreover, its frequency of 100 percent indicates an even distribution, as it appears visually, over the entire area of sampling. This is a dense or closed forest.

Scattered monadnocks of lava, which rise through the mantle, support the remaining species. Also, up the lee slope of Nash Crater, the forest is predominately lodgepole pine; however, the orographic effect overcomes the substratal condition enough to allow yellow pine, Douglas fir, and grand fir to come in.

The relation of lodgepole pine to the other species is shown strikingly in the summed quantitative data of the synusia's phytographs (Fig. 8). Neither Douglas fir, western yellow pine, nor grand fir can be considered as union subdominants since they are active not in the community but only on lava outcrops included in the area of community control. In addition, lodgepole pine has a high reproductive capacity and a preponderance of trees in the lower size classes (Table 9). This phenomenon is indicative of both early consolidation and of the unfavorableness of the area for quantitative growth. Most lodgepole pines complete their short life cycle never reaching more than 2 to 4 inches in diameter.

Fig. 8. Phytographs of the arborescent species of the *Pinetum contorti lapillosum* association. Legend the same as for Fig. 5.

Table 9. Size class distribution of the abundance of the arboreal species of the *Pinetum contorti lapillosum* association.

Species	Repr.	−3	−6	−12	−24	+24	Total
Pinus contorta var. *murrayana*	426	757	200	173	4	0	1560
Pseudotsuga taxifolia	16	7	5	3	0	1	32
Pinus ponderosa	4	1	1	2	1	0	9
Abies grandis	27	1	1	0	1	0	30
Tsuga mertensiana	2	0	0	1	0	0	3
Abies amabilis	1	0	0	0	0	0	1
Tsuga heterophylla	1	0	0	0	0	0	1
Pinus monticola	..	..	..	..	..	..	..

Size (diameter) Classes—Inches

THE FRUTESCENT SYNUSIA: CEANOTHUS VELUTINUS
UNION

Two constants are distinctive in this union. Presumably they have almost the same ecologic amplitudes in this region as lodgepole pine. The dominant is *Ceanothus velutinus* which reaches greatest cover in the higher flats where it forms almost impenetrable thickets (Table 8). Near Little Nash, however, the union is absent under the broken scrub lodgepole pine stand. In addition to *Ribes viscosissimum*, which is a subdominant associated with *Ceanothus velutinus*, the remaining species occur with the arborescent elements on the lava outcrops. One exception, *Juniperus communis* var. *sibirica*, subsists as a small mat at the top of the southeast rim of Nash Crater.

THE HERBACEOUS SYNUSIA: CAREXETO-PENSTEMON
UNION

Quite a different herbaceous flora is associated with this xeric, sterile habitat. Many of the species are apparent invaders from eastern Oregon deserts. Two species, *Carex inops* and *Penstemon confertus* var. *procerus*, have sufficient combined quantitative values and presence to be considered as dominants (Table 8). Their values of density and frequency are relatively low; however, this is because of their poor development on the flats around Santiam Highway Junction. At the lowest stand along the highway and west of Little Nash Crater, they form a dense cover. On the high benches at the base of Nash Crater, *Fragaria bracteata* is ascendant. The latter's incomplete presence excludes it as a union constant, or association type species. *Lomatium angustatum*, *Eriogonum* spp., *Haplopappus greenii*, *Spraguea umbellata*, *Aster radulinus*, and *Lupinus lyallii* occupy the most xeric sites. These occur in no other sere on the flows.

THE BRYOPHYTIC SYNUSIA: POLYTRICHUM
JUNIPERINUM UNION

One moss, *Polytrichum juniperinum*, prevails on the ash and lapilli. Its low frequency (22) describes its inconsistent establishment. The other species, *Rhacomitrium patens* and *R. lanuginosum*, are, as before, associated only with the lavas and hence occur on the scattered projecting knolls.

INTERRELATIONS OF THE COMMUNITY

The affinities of this association are distinct and separate from those associations which border it. The very nature of the environmental complex to which its flora is adapted and an absence of infiltration, except upon lava knolls within its area, distinguishes the area of control as a primary sere. Clearly, lodgepole pine and its associated species are primary invaders. They have, so far, altered the environment but little to allow their replacement. Dead Douglas fir seedlings are diffused throughout the forest, but no active establishment, not associated with the presence of lava, is apparent.

Over much of the area of the association there is a loose social organization. In the more mesic portions of the flats, *Ceanothus velutinus* forms a thick layer under the open lodgepole pine canopy; and beneath it, a verdant mat of *Penstemon confertus* var. *procerus*, *Carex inops*, and *Eriogonum augustifolium* covers the ground. Yet it is doubtful if the lower layers owe their existence to, or are altered by, the lodgepole pine canopy. The thin soil and poor aeration do not preclude active competition. Growing conditions are at their best, as is reflected in the herbs themselves.

Primary succession and the youth of the sere are both confirmed in the inconsistencies and in the proportion of species in the A and B columns of the frequency diagrams (Fig. 9). Also, phenologic peaks are evident in the data of Table 10. Two herbaceous species, *Spraguea umbellata* and *Lomatium angustatum*, form a sparse prevernal-vernal aspect. The bulk of the species commence flowering in the late vernal and estival periods. Several species, mostly composites, are autumnal.
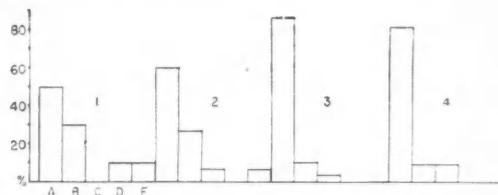
FIG. 9. Frequencies of the synusiae of the *Pinetum contorti lapillosum* association. Legend the same as for Fig. 4.

THE CAREXETO-VACCINETUM OCCIDENTALIS
ASSOCIATION

THE FRUTESCENT SYNUSIAE: SALIX UNION AND
VACCINIUM OCCIDENTALIS UNION

The high lava dam at Big Spring Bog marks the end of a flow which cut off a small intermittent drainage line. Its fan defines the crescent shape of the resultant bog, and it receives back again into its lip a limited drainage to the west. The *Aceretum circinati lavosum* on these lavas marks the southern boundary of the small palustrophytic association; and around the outer periphery of the crescent to the north, east, and west the *Pseudotsugetum taxifoliae tsugosum* on glacial till crowds down to the marginal ditch.

Two well defined shrub unions are quite separate over the bog. Around the shallower edges, a dense thicket or rim of *Salix scouleriana* and *S. piperi* extends 30 feet towards the bog center. At the very edge of the slightly formed marginal ditch, and on soil, a thin scattering of *Alnus sinuata* rings the outer circumference of this union. Mixed in with the willow are *Sambucus racemosa* var. *callicarpa*, *Amelanchier florida*, and *Spiraea douglasii* var. *menziesii* with individuals of *Lonicera involucrata* var. *ledebourii* along its inner periphery. The second union, the Vaccinium occidentalis union, occupies the center and greater part of the bog on the deep, sedge-peat, intrazonal substrate (Fig. 10).

TABLE 10. Phenology of the shrubs and herbs of the *Pinetum contorti lapillosum* association for the growing season of 1949 from the middle of May to the last of September.

Species	Months				
	May	June	July	Aug.	Sept.
SHRUBS					
Ceanothus velutinus	- - - -	- † x x	x x ‡ 0	0 0 0 0	0 0 0
Ribes viscosissimum	- - - -	- - - -	x x ‡ ‡	0 0 0 -	- - -
Pachistima myrsinites	- - - x	x ‡ ‡ ‡	‡ ‡ ‡ ‡	‡ ‡ ‡ ‡	‡ ‡ ‡
Arctostaphylos nevadensis	- - - x	x x x ‡	‡ ‡ ‡ 0	0 0 0 0	0 0 0
Rubus parviflorus	- - - -	- - - x	x x x ‡	‡ ‡ 0 0	0 - -
Prunus emarginata	- - - -	- x x ‡	‡ 0 0 0	0 0 - -	- - -
Rhamnus purshiana	- - - -	- - - -	x ‡ ‡ 0	0 0 0 0	? ? ?
Salix sp.	- - - -	- - - -	- - - -	- - - -	- - -
Holodiscus glabrescens	- - - -	- - - -	- - - †	x ‡ ‡ 0	0 0 0
Castanopsis chrysophylla	- - - -	- - - -	- - † x	x ‡ ‡ 0	0 0 0
HERBS					
Carex inops	- - - -	- x x 0	0 0 0 0	- - - -	- - -
Penstemon confertus var. procerus	- - - -	- - - x	x ‡ ‡ ‡	‡ 0 0 0	0 0 0
Epilobium angustifolium	- - - -	- - - -	† x x ‡	‡ ‡ ‡ ‡	0 0 0
Fragaria bracteata	- - - -	- - x x	x x ‡ ‡	0 0 - -	- - -
Stipa thurberiana	- - - -	- x x 0	0 0 0 0	0 - - -	- - -
Sitanion hystrix	- - - -	- x x 0	0 0 - -	- - - -	- - -
Pedicularis racemosa	- - - -	- - - -	- - - x	x x ‡ ‡	‡ 0 0
Lomatium angustatum	- - - x	x ‡ ‡ ‡	‡ ‡ ‡ ‡	‡ 0 0 0	0 0 0
Eriogonum nudum	- - - -	- - x x	x x x x	‡ ‡ ‡ 0	0 - -
Hieracium greenii	- - - -	- - - -	- - x x	x ‡ 0 0	0 0 -
Eriogonum marifolium	- - - -	- - x ‡	‡ ‡ ‡ ‡	‡ 0 0 0	0 - -
Penstemon menziesii var. davidsonii	- - - -	x x x ‡	‡ ‡ 0 0	0 0 0 0	0 0 0
Arenaria macrophylla	- - - -	- - x x	x x x x	‡ ‡ ‡ 0	0 - -
Clintonia uniflora	- - - -	- - † x	x ‡ ‡ ‡	‡ 0 0 0	0 0 0
Achlys triphylla	- - - -	† x x ‡	‡ 0 0 0	0 0 0 0	0 - -
Haplopappus greenii	- - - -	- - - -	- - † x	x ‡ ‡ ‡	‡ 0 0
Pyrola secunda	- - - -	- - - -	- - † x	‡ ‡ ‡ ‡	‡ ‡ ‡
Spraguea umbellata	- - x x	x x ‡ 0	0 0 - -	- - - -	- - -
Lupinus lyallii	- - - -	- - x ‡	‡ ‡ ‡ ‡	‡ 0 0 0	0 0 -
Pyrola dentata	- - - -	- - - -	- † x x	x ‡ ‡ ‡	0 0 0
Chimaphila umbellata var. occidentalis	- - - -	- † † †	† † x x	x ‡ ‡ ‡	0 0 0
Sedum oregonense	- - - -	- † † x	x x x ‡	‡ ‡ 0 0	0 - -
Eriogonum pyrolaefolium var. coryphaeum	- - - -	- x x x	x x x ‡	‡ ‡ ‡ 0	0 0 0
Anaphalis margaritacea	- - - -	- - - x	x x x ‡	‡ ‡ ‡ ‡	‡ 0 0
Arabis holboellii var. secunda	- - - -	x ‡ ‡ ‡	‡ ‡ ‡ 0	0 0 - -	- - -
Aster radulinus	- - - -	- - - -	- - - x	x x ‡ ‡	‡ ‡ 0
Arabis lyallii			—no record—		

- floral inactivity; † in bud; x flowering; ‡ flowering and fruiting; ? unknown

A single sampling transect of 16 quadrats was used to define area control rather than separate union control. The results in Table 11 show the great consolidation of *Vaccinium occidentalis* portrayed in Fig. 10. A density or unit area abundance of 15, a frequence of 81 percent are low for its union. Here it is the only shrub. For the bog as a whole it is the dominant. Of the remaining shrubs which compose the Salix union, *S. scouleriana* and *S. piperi* have the superior quantitative values.

THE HERBACEOUS SYNUSIA: CAREX SITCHENSIS UNION

In this lower stratum, there is a grouping as in the shrub layers. *Smilacina sessilifolia*, *Glyceria pauciflora*, *Mimulus dentata*, *Calamagrostis canadensis*, and *Cicuta douglasii* are present only beneath the willow cover. However, this synusia comprises

FIG. 10. Big Spring Bog occupied by the *Carexeto-vaccinetum occidentalis* association. The Salix union forms a peripheral band around the inner edge of the bog. The inner portion is made up of a dense cover of *Vaccinium occidentalis* and *Carex sitchensis*. In the background, the climax forest descends to the marginal ditch—Photo by C. Heusser (May 1950).

only one union since elements of the open bog extend into this zone. Most of the above species are expressly helophytes confined to the shallow water and swampy conditions of the marginal ditch.

Over the bog *Carex sitchensis* dominates the union; its high frequence (87) and density (20.2) also bring into relief its sociologic position since it grows as high as *Vaccinium occidentalis* (Table 9). It is easily the superior plant regardless of life form, and thus, may be considered a co-dominant with *Vaccinium occidentalis* in designating the association.

In open patches of water, *Carex rostrata*, *Juncus filiformis*, and *Potential palustris* predominate. Only *Carex rostrata* is present on the slightly higher peat with *Carex sitchensis*. Scattered individuals of *Agrostis thurberiana* (frequency 37; density 0.9), and *Habenaria leucostachys* (f. 25; d. 0.2) are associated with the closed cover.

INTERRELATIONS OF THE COMMUNITY

The chemico-physical factors which typify a bog environment define a rather select and quite different flora in any region. Therefore, it is not surprising that in this association few or no affinities with surrounding associations are visible in the species list.

TABLE 11. Phytosociologic data of the Salix and Vaccinium occidentalis unions and the Carex sitchensis union of the *Carexeto-vaccinetum occidentalis* association. The former are of the frutescent synusia and the latter of the herbaceous. Life form designations as in Table 1.*

| Species | QUANTITATIVE | | | | | QUALITATIVE |
| | Density | | Frequency % | Cover | | Life Forms |
	Relative	% Total		sq. m.	% Total	
SHRUBS						
Vaccinium occidentalis	15.00	81.7	81	36.0	79	Ph
Salix scouleriana	0.88	4.8	6	3.2	7	Ph
Salix piperi	1.31	7.2	12	2.1	5	Ph
Alnus sinuata	0.18	1.0	6	2.0	4	Ph
Sambucus racemosa var. callicarpa	0.25	1.4	6	1.2	3	Ph
Lonicera involucrata var. ledebourii	0.44	2.4	12	0.3	1	Ph
Amelanchier florida	0.25	1.4	6	0.4	1	Ph
Spiraea douglasii var. menziesii	0.06	0.3	6	0.0	0	Ph
HERBS						
Carex sitchensis	20.25	64.0	87	...	..	Cr
Smilacina sessilifolia	1.62	5.1	21	...	..	Cr
Agrostis thurberiana	0.88	2.6	37	...	..	H
Potentilla palustris	1.75	5.5	6	...	..	Cr
Carex rostrata	2.63	8.3	12	...	..	Cr
Juncus filiformis	1.25	3.9	6	...	..	Cr
Carex disperma	...	....	..	...	..	H
Carex leptopoda	1.37	4.3	6	...	..	Cr
Habenaria leucostachys	0.31	1.6	25	...	..	H
Glyceria pauciflora	0.31	1.6	6	...	..	Cr
Mimulus dentata	0.31	1.6	12	...	..	Cr
Carex sp.	0.31	1.6	6	...	..	Cr
Calamagrostis canadensis	0.5	2.5	6	...	..	Cr
Cicuta douglasii	0.13	0.4	12	...	..	H
Mimulus primuloides	...	....	..	...	..	Cr
Hypericum anagalloides	...	....	..	...	..	H

*Two lodgepole pine were growing in the bog but were not sampled; the bryophytic layer was composed of a solid mat of *Rhacomitrium* sp. without sporophytes.

The lack of active hydrarch succession to the higher forest units illustrates the youth of the bog. The physiography of the basin and the drainage pattern both discount a raising of the water and peat levels to heights much above those of the present. Undoubtedly then, incoming sediments will soon fill in the bog, lower the water table, and forest encroachment will take place.

Within the association, one change is occurring. The few remaining, small spaces of open water are being filled in gradually by sedge peat, closely followed by *Vaccinium occidentalis* and *Carex sitchensis*. The extent of the willow band seems fixed by the depth of the substrate around the shore line. Conceivably, as the bog fills in, this band will cover over the peat and be followed by the climax forest stage.

The frequency charts reveal, in both synusiae, wide gaps in the middle of the spectrum (Fig. 11). This is a primary sere in its first stages of development prior to fluctuation and replacement.

Throughout the short spring and into summer, the bog is covered with water from the melting snows. Drainage is slow and only in late summer and early autumn does the outflow lower the water table down
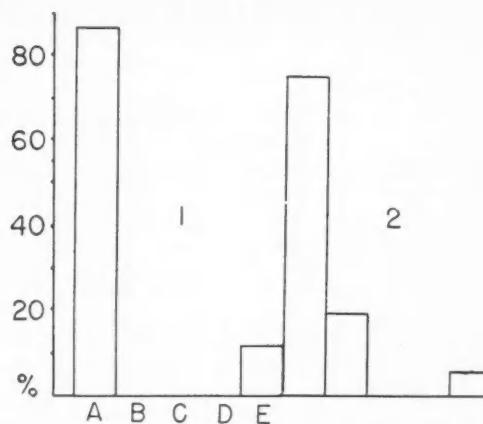
FIG. 11. Frequency graphs of the unions of the *Carexeto-vaccinetum occidentalis* association. Legend same as for Fig. 2.

into the peat. This is particularly reflected in the phenology of the lower life forms (Table 12). Their life cycles are often quite short but must vary from year to year depending upon the depth of the snow pack and variances of the factors which affect its melting.

Vernal species such as *Salix piperi* and *Salix*

TABLE 12. Phenology of the shrubs and herbs of the *Carexeto-vaccinetum occidentalis* association for the May-September growing season of 1949.

| Species | MONTHS | | | | |
	May	June	July	Aug.	Sept.
SHRUBS					
Vaccinium occidentalis	- - - -	- - - x	‡ 0 0 0	0 0 0 0	0 0 -
Salix scouleriana	- - - -	- - - x	x 0 - -	- - - -	- - -
Salix piperi	- - - -	- - - x	x 0 - -	- - - -	- - -
Alnus sinuata	- - - -	—no record —			
Sambucus racemosa var. callicarpa	- - - -	- - x x	x ‡ ‡ 0	0 0 0 0	0 0 0
Lonicera involucrata var. ledebourii	- - - -	- - - x	x ‡ ‡ ‡	0 0 0 0	0 0 0
Amelanchier florida	- - - -	- - x x	‡ ‡ ‡ 0	0 0 0 0	0 0 0
Spiraea douglasii var. menziesii	- - - -	- - - -	- † † x	x x ‡ ‡	0 0 0
HERBS					
Carex sitchensis	- - - -	- - x x	‡ 0 0 0	0 0 - -	- - -
Smilacina sessilifolia	- - - -	- † x x	x ‡ ‡ 0	0 0 0 -	- - -
Agrostis thurberiana	- - - -	- - x x	0 0 0 -	- - - -	- - -
Potentilla plaustris	- - - -	- - - †	x x x	‡ ‡ 0 0	0 0 0
Carex rostrata	- - - -	- - - -	x x ‡ ‡	0 0 0 0	- - -
Juncus filiformis	- - - -	- - - x	x ‡ 0 0	0 - - -	- - -
Carex disperma	- - - -	—no record—			
Carex leptopoda	- - - -	—no record—			
Habenaria leucostachys	- - - -	- - - -	- - † x	x ‡ ‡ 0	0 - -
Glyceria pauciflora	- - - -	- - - -	- - † x	x 0 0 0	0 - -
Mimulus dentata	- - - -	- - - -	- - x x	‡ ? ? 0	0 - -
Carex sp.	- - - -	—no record—			
Calamagrostis canadensis	- - - -	- - - -	- - † x	x 0 0 0	0 - -
Cicuta douglasii	- - - -	- - - -	- - - -	x x x ‡	‡ ‡ 0
Mimulus primuloides	- - - -	- - - -	- - - -	- - - x	x x ‡
Hypericum anagalloides	- - - -	- - - -	- - - -	- - - x	‡ ‡ ‡

- floral inactivity; † in bud; x flowering; ‡ flowering and fruiting; 0 fruiting; ? unknown.

scouleriana flowered behind those of other associations. Many herbs were pushed into autumnal phase by the high water, including *Mimulus primuloides*, *Hypericum anagalloides*, and *Cicuta douglasii*.

THE PSEUDOTSUGETUM TAXIFOLIAE TSUGOSUM ASSOCIATION

THE ARBORESCENT SYNUSIA: PSEUDOTSUGETO-TSUGA UNION

Many thousands of years separate this forest union from those of the developmental associations.

TABLE 13. Phytosociologic data of the Pseudotsugeto-tsuga, Roseto-vaccinium, and Linnaeto-cornus unions and the bryophytes of the *Pseudotsugetum taxifoliae tsugosum* association. These are the arborescent, frutescent, and herbaceous synusiae respectively. Presence, stations A—between North Santiam Highway and Big Spring Bog: B—Clear Lake Junction; C—Lava Lake. Life form designations as in Table 1.

	QUANTITATIVE					QUALI-TATIVE	SYN-THETIC
Species	Density		Frequency %	Space		Life Forms	Presence Stations A B C
	Relative	% Total		Basal Area sq. in.	% Total		
TREES							
Pseudotsuga taxifolia	2.08	5.2	92	26,219	83	Ph	x x x
Tsuga heterophylla	16.50	41.0	75	1,164	4	Ph	x x x
Abies amabilis	16.70	41.4	83	2,262	7	Ph	x x x
Abies grandis	2.33	5.8	50	1,005	3	Ph	x x x
Pinus monticola	0.42	1.0	16	901	2	Ph	x x x
Taxus brevifolia	2.33	5.8	25	28	0	Ph	- x -
Picea engelmanni	....	....	..			Ph	- - x
SHRUBS				Cover (sq.m.)			
Vaccinium membranaceum	8.42	40.6	58	1.5	40	Ph	x x x
Rosa gymnocarpa	3.58	17.6	83	0.2	4	Ph	x x x
Rubus vitifolius	1.41	6.8	42	0.1	2	Ch	x x x
Pachistima myrsinites	3.50	16.9	50	0.7	19	Ph	x - x
Acer circinatum	0.75	3.6	15	0.6	15	Ph	x - x
Berberis nervosa	2.66	12.8	25	0.3	8	Ch	- x x
Amelanchier florida	0.33	1.6	8	0.4	10	Ph	- x -
Castanopsis chrysophylla	0.08	0.4	8	0.0	0	Ph	- x -
HERBS							
Linnaea borealis var. americana	7.66	25.3	83	....	..	Ch	x x x
Cornus canadensis	6.66	22.0	58	....	..	Cr	x x x
Achlys triphylla	4.00	13.2	66	....	..	H	x x x
Chimaphila umbellata var. occidentalis	3.58	11.8	58	....	..	Cr	x x x
Clintonia uniflora	2.41	7.90	58	....	..	Cr	x x x
Trillium ovatum	0.42	1.4	25	....	..	Cr	x x x
Anemone deltoidea	0.42	1.4	25	....	..	H	x x x
Viola glabella	0.58	1.9	16	....	..	Cr	x x x
Goodyera decipiens	0.16	0.5	8	....	..	Cr	x x x
Anemone oregana	0.16	0.5	8	....	..	H	x x x
Allotropa virgata	....	....	..	....	..	Cr	x x x
Corallorhiza mertensiana	....	....	..	....	..	Cr	x x x
Smilacina sessilifolia	1.25	4.1	25	....	..	Cr	x - x
Xerophyllum tenax	0.33	1.1	8	....	..	H	x - x
Pyrola aphylla	....	....	..	....	..	Cr	x x -
Pyrola secunda	0.92	3.0	25	....	..	Cr	x x -
Tiarella unifoliata	1.00	3.3	16	....	..	H	x x -
Pyrola bracteata	0.50	1.7	8	....	..	Cr	x x -
Fragaria bracteata	0.33	1.1	8	....	..	H	x - -
Chimaphila menziesii	....	....	..	....	..	Cr	x - -
Listera convallarioides	....	....	..	....	..	H	x - -
Adenocaulon bicolor	....	....	..	....	..	Cr	x - -
Disporum oreganum	....	....	..	....	..	H	x - -
MOSSES							
Rhytidiadelphus triquetrus	....	....	8	0.1	87	H	x x x
Bryum miniatum	....	....	8	0.02	13	H	- x x

The substrate is deep and rich. The canopy is closed and the forest floor is dark and bare. Species are present whose seedlings will develop in a very low intensity of light and perpetuate themselves indefinitely. This closed stratum ameliorates environmental extremes. Mesism, competition, sciophytic dependence, are all characteristic of its composition. This is the middle montane climax forest of the Cascades.

The total sampling and the quantitative data obtained therefrom are neither indicative of the entire association nor in part of this entire union since the association extends over many square miles on both sides of the Western Cascades. Three stations were selected around its peripheral convergence with the lava associations. The data from these stations serve, however, as a comparison with the Nash Crater lava communities, and are indicative of at least a part of the association.

In 12 quadrats, a basal area of 26,219 square inches, which is 83 percent of the total basal area of all species, was recorded for Douglas fir (Table 13). In addition, these figures are from but 25 individuals. Its high frequence of 93 and density of 2.1, together, show its dominance.

Western hemlock and lovely fir both have a density of 16.5 and a high frequency of 75 and 83 respectively. However, their basal areas are low in relation to that of Douglas fir and were but 4 and 7 percent of the total respectively. The distribution of abundances in the various size classes is depicted in Table 14. Since western hemlock has trees in the larger size classes, high density, and frequency, it is also considered as a dominant of this stratum.

TABLE 14. Size class distribution of the abundance of the arboreal species of the *Pseudotsugetum taxifoliae tsugosum* association.

Species	SIZE (diameter) CLASSES—INCHES						
	Repr.	−3	−6	−12	−24	+24	Total
Pseudotsuga taxifolia	16	7	5	3	0	1	25
Tsuga heterophylla	181	1	4	4	5	3	198
Abies amabilis	163	13	11	7	6	0	200
Abies grandis	14	1	6	3	4	0	28
Pinus monticola	3	0	0	0	1	1	5
Taxus brevifolia	23	3	2	0	0	0	28
Picea engelmanni	..	...	..	..	..	..	..

These size class data also reveal that western hemlock is aggressive; whereas, though the Douglas fir are large, abundant, and homogeneous in distribution, their reproduction is negligible, and thus they are playing less and less of an active part in the sociology of the union.

Grand fir and white pine are the other two association type species of this union. Their sociologic data denote them as subdominants. Yew *(Taxus brevifolia)* is found only in the most consolidated portions of the forest as a scattered microphanerophyte. One Englemann spruce was encountered in reconnaissance.

THE FRUTESCENT SYNUSIA: ROSETO-VACCINIUM UNION

Three constants typify this union and do not seem to be dependents of the closed forest conditions, but rather tolerants. *Vaccinium membranaceum, Rosa gymnocarpa, Rubus vitifolius,* and *Berberis nervosa* form a discontinuous stratum, except in openings of the forest, or at its edges. In the deep forest, their quantitative growth form is weak, their vitality low.

The most widely distributed shrub is *Rosa gymnocarpa* (frequency 83); whereas, *Vaccinium membranaceum*, though occurring in patches (frequence 58), has higher density 8.4 and cover (40% of the total values) (Table 13). These shrubs together may be more-or-less considered as co-dominants of this poorly defined union. The other species occur only at the edge of the forest adjacent to the lavas, where the light is sufficient for their survival.

THE HERBACEOUS SYNUSIA: LINNAETO-CORNUS UNION

The richness of species development marks this union (Table 13). Many are constants of high vitality at all stations dependent upon climax forest coaction and reaction.

Twinflower *(Linnaea borealis* var. *americana)* forms a scattered mat over much of the forest floor (density 7.6; frequency 83). Associated with it, to a lesser extent, *Cornus canadensis* has a high consolidation except in the older portion of the forest at Clear Lake Junction. Also, many species as *Achlys triphylla* and *Clintonia uniflora* have a similar distributional pattern.

Such sciophytic saprophytes as *Allotropa virgata, Corallorhiza mertensiana,* and *Pyrola aphylla* are dependent upon the duff accumulation, high soil moisture efficiency, and shade afforded by the old, closed arborescent stratum. Other species as *Chimaphila menziesii, Listeria convallarioides, Adenocaulon bicolor,* and *Disporum oreganum* grow in more open sites.

INTERRELATIONS OF THE COMMUNITY

The dynamics and state of syngenetical development are graphically illustrated in the photographs (Fig. 12) and size-class table. The large-sized Douglas fir do not reproduce and will evidently be replaced by the aggressive species, western hemlock, and lovely fir. The structural relationships also suggest that the glacial tills were first occupied by Douglas fir. The few large western hemlock further suggest a limited infiltration. But as reaction proceeded, the degree of consolidations increased to a point of present dominance by the mesic species. In proportion, few Douglas fir were able to seize and only a high abundance of rather early individuals now remains.

Definite social structure is visible in the number of species which could exist only in this deep forest environment. In places where cover is very dense, stratification breaks down, competition and certain physical minima are too severe, and only saprophytes are present. Yet these species are the complement of a stable terminus, irreplaceable outside of
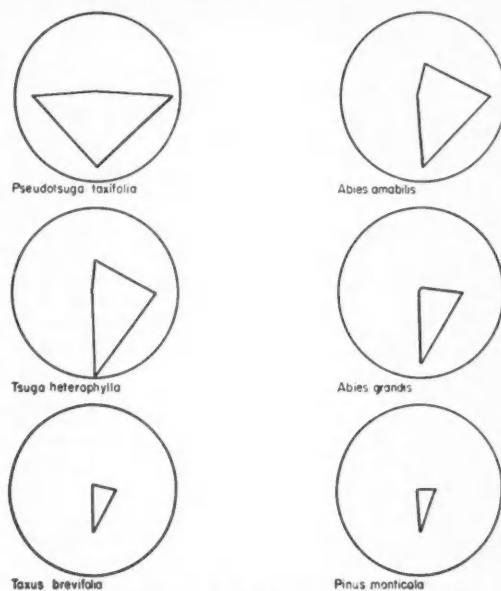
FIG. 12. Phytographs of the arborescent stratum of the *Pseudotsugetum taxifoliae tsugosum* association. Legend same as for Fig. 5.

disturbance, and they make up a closely knit aggregation.

Furthermore, the extreme to which consolidation has taken place is shown in the frequency plots (Fig. 13). When compared to a "normal," class E, indicative of climax dominants, is very high; class A, indicative of invaders or of the unstable portion of a flora, is very low. The poor development of the Roseto-vaccinium union is reflected in the frutescent plot, though class E is represented and class A is low. Normality is approached in the herbaceous stratum.
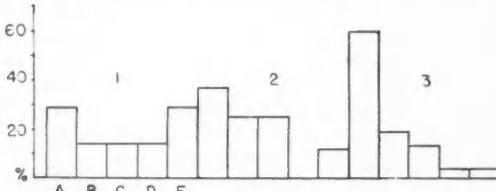
FIG. 13. Frequency graphs of the synusiae of the *Pseudotsugetum taxifoliae tsugosum* association. Legend same as for Fig. 4.

With the exception of *Berberis nervosa*, the shrubs were unable to complete their life cycles in the dense forest at Clear Lake Junction. Along the highway and around clearings or in a thinning of the stand, as at Lava Lake and Big Spring stations, the remaining constants were quite vigorous. Phenologic data or the plants of this association show no conspicuous lag behind their cycles where they have occurred in other forest associations.

SYNGENETICAL TRENDS

A series of young priseres such as these presents a study of long-range dynamics. Interchange, extinction, and invasion are slow-acting forces. The associations retain their primary integrity; and allegoric logic, not the scanty evidence, is the only index of the probable direction of future change.

Undoubtedly three of the associations are primary seres: the block basalts of the *Aceretum circinati lavosum;* the peats of the *Carexeto-vaccinetum occidentalis;* and the ash-lapilli mantle of the *Pinetum contorti lapillosum.* Their species lists denote their individuality in that there are no species present which would replace the constants when the latter's reaction alters the present environments to make such invasion possible. Conceivably in an indeterminate lapse of time all three seres will be replaced by the regional climax, the Douglas fir-hemlock association.

A thread of species interchange links together directly four associations. The herbaceous and frutescent species of the *Aceretum circinati lavosum* also make up the understory of the *Pseudotsugeto-abietum lasiocarpae;* and in the *Pseudotsugeto-abietum lasiocarpae* are sparingly established a few seedlings and small trees of species which play dominant and subdominant roles in the *Pseudotsugeto-abietum grandis.* In the *Pseudotsugeto-abietum grandis,* the major species of the preceding association occur sparsely, and climax species from the *Pseudotsugetum taxifoliae tsugosum* are mixed in to a slight degree in the more mesic stands on the slopes of Nash Crater.

From these indications, there might possibly be an orderly chain of progression, as reaction proceeds, from the *Aceretum circinati lavosum* through the *Pseudotsugeto-abietum lasiocarpae* to the *Pseudotsugeto-abietum grandis* to the regional terminus, the *Pseudotsugetum taxifoliae tsugosum.* It is possible that the *Pseudotsugeto-abietum lasiocarpae* was preceded by the *Aceretum circinati lavosum* or the *Pseudotsugeto-abietum grandis* by the former. But on the other hand the lavas are young, the individual aggregations are bound by distinct environmental differences, and since only traces of reaction are visible, such as a slight soil development in some portions of the *Pseudotsugeto-abietum grandis,* the associations may have become established initially on the lavas much as they are at the present.

The individualistic complements of the remaining associations show no syngenetic associations. It seems probable that eventually the climax forest will replace the *Carexo-vaccinetum occidentalis* since it all but surrounds it. Infiltration should occur as the bog fills and drys up. The nature of the primary stages of replacement of, or succession onto, the ash-lapilli flats, however, is questionable. A vast number of substratal alterations will be necessary by countless generations of lodgepole pine before limited infiltration commences. Possibly, climax forest species will be able to come in along with components of the *Pseudotsugeto-abietum grandis.* Undoubtedly, though, an arborescent cover of Douglas fir will first dominate, and since lava is absent, the lower synusiae of the climax forest will become established on the new soil. Many paleochronologic studies by Hansen of postglacial forest successions in the Pacific Northwest give evidence of a rather constant pattern of change. One such pollen record sequence in the Puget Sound Lowlands (Hansen 1949) demonstrated that lodgepole pine occupied deglaciated terrain in the wake of retreating ice, and after sufficient edaphic stability had been attained was invaded by both Douglas fir and hemlock. And since these two species are of greater longevity, stature, and are more tolerant to shade, they replaced the initial lodgepole pine forests. His chronologies further show that if such an area is left undisturbed by fire, disease, or cutting for five or six centuries, the less tolerant Douglas fir is almost entirely replaced by western hemlock and other climax dominants.

THE BIOLOGICAL SPECTRUM OF THE TOTAL VEGETATION

Life-form analyses may best complete an overall floristic expression of an area solely on a physiognomic basis. Therefore, the life-form spectrum of the collective associations and its class percentages was derived from the life-form designations appended to each species in the association lists. Also included in this analysis are a number of ruderals which do not appear on the association lists since they are restricted to the roadsides, Fish Lake picnic ground, and to the Remount Station dump ground.

The climate of the Nash Crater region is largely cryptophytic (Table 15). Its cryptophytic percentage of 29 strongly exceeds that of the normal (6).

TABLE 15. The life-form spectra of Nash Crater lava flows, other Northwest Pacific areas, and the world normal. Life form designations as in Table 1.

Region	Species	PERCENTAGE DISTRIBUTION OF SPECIES				
		Ph	Ch	H	Cr	Th
Nash Crater Lava Flows...	174	20.0	5.0	42.0	29.0	3.0
Cascade Range..	...	10.2	9.5	35.8	37.2	7.3
Oregon..........	...	9.6	6.3	37.3	25.3	21.3
Mary's Peak....	...	19.0	2.0	54.0	25.0	0.0
Normal Spectrum.....	...	46.0	9.0	26.0	6.0	13.0

There is also a significant increase in the hemicryptophytes of the area, 42 as compared to 26 percent for the normal. Such a high percentage of cryptophytes with a relative, corresponding low percentage of chaemophytes has been broadly interpreted as characteristic of temperate climates (Oosting 1942). Nevertheless, northern affinities are present, and edaphic and geologic factors, in addition to climate, produce a variety of habitats and associated species in this region. A cryptophytic climate, not recognized by Raunkiaer (1934), would seem more appropriate of a high latitude or orographic vegetation. The spectrum of Mary's Peak (Merkle 1951),

the highest in Oregon's coast range represents strong boreal similarities modified by maritime influence and has much the same trends as are shown in the Nash Crater spectrum. The difference between these two in the therophytic class probably reflects the xeric influence in the latter.

Undoubtedly the Nash spectrum is quantitatively distorted because of the wide range of habitat variation from the priserie aggregations to the closed forest. Yet it does show, as do other associated forest spectra from Oregon (unpublished data, H. P. Hansen), a broad manifestation, well within regional amplitudes, of a maritime modification of high latitude or boreal climate through its hemicryptophyte-cryptophyte ratio.

ENVIRONMENTAL ANALYSIS

MICRO-CLIMATIC FACTORS

The mean average precipitation of 50 inches has a relatively high effectivity since there are high humidities even during the dry summer months. Likewise, the regional temperatures are moderate, since they are tempered during the winter by marine influence, the snow pack, and by the exclusion of Continental Polar air by the High Cascades and Rockies. However, this regional orographic pattern is altered in the Santiam region somewhat by degrees of forest consolidation, substrate, and, to a lesser extent, topography. These variations are shown in part by the temperature and humidity data of two stations, which were maintained during the growing season in the two extremes of habitat diversity—the open lava and the climax forest (Table 16). These data show that during the most effective portion of the growing

TABLE 16. Highest maximum and lowest minimum temperatures and relative humidities within the climax forest and in the open lava at ground level for most of the growing season of 1949.

Period Station	Temperatures								Humidities		
	Maximum				Minimum						
	Night		Day		Night		Day		Max.	Min.	Aver.
	H	Aver.	H	Aver.	L	Aver.	L	Aver.			
June 25 to 30											
Lava	75	72	73	63	46	48	46	55	100	32	70
Forest	59	53	62	54	38	40	42	46	100	52	82
July 1 to 15											
Lava	99	88	107	103	48	51	50	65	74	15	41
Forest	80	72	90	80	48	48	48	59	84	40	62
July 15 to 31											
Lava	68	63	85	70	46	51	54	58	100	47	73
Forest	76	77	84	75	44	48	50	58	100	53	84
August 1 to 15											
Lava	74	72	96	81	48	51	55	62	70	40	54
Forest	60	59	62	59	40	45	50	60	79	62	70
August 15 to 31											
Lava	75	73	86	79	40	45	54	60	60	40	51
Forest	64	63	66	61	42	45	54	56	72	53	64

season, which is in late May, maximum temperatures are lower in the forest, the nighttime difference is 19° F and the daytime difference is 9° F. At this time ground moisture supply and melt water runoff are high still and the lava mass is relatively cool. In the first half of July, however, the diurnal ranges become greater. The night and day differentials are 16 and 23 degrees respectively. Also, the day maximum average is 103° in the lavas for these 15 days. Minimum temperatures are always lower in the forest; and there is less of a range between maxima and minima in the forest than in the lavas.

Even though summer precipitation is very low, the humidity data reflect foggy and light rain interims during the summer, a condition already shown in the regional data. On an average, they are fairly high over the lavas, but always lower than those of the forest, in spite of their high air temperatures.

These trends are probably accountable both to, or to the lack of, a heavy forest cover, and to the insolation absorptive capacity of the black lava. Beneath a shaded canopy, evaporation is reduced, temperatures are more stable, and soil moisture is more effective. In both stations and for the region as a whole, air movement is notably absent so that evaporation. as reflected by humidities, is more a function of temperature.

EDAPHIC FACTORS

The entire substratal complex, from the ash covered glacio-fluvial soil to the block basalts and the deep ash-lapilli mantle, manifests extreme youth in addition to the proposed volcanic chronology, for in the profile ratios inherited characters far out weight acquired ones. Parent material is evident at all stations, and under even the climax forest the older vegetation and the regional climate have not produced a stabilized mature soil or montane podzol.

The typical profile of the *Pseudotsugetum tarifoliae tsugosum* is one only recently altered by ash deposition. Ao1, o2, o3, layers are barely defined, but humus has become incorporated into two feet of still-yellow ash to form an A1. Profile layers below this depth are not discernible in the coarse yellow glacial till. However, this substrate is deep. At ten feet it grades into hard gray clays, and thus provides an adequate substrate and root zone for the larger species.

The profile of the *Aceretum circinati lavosum* is one of large black blocks with large air crevices between; there is no soil, no profile formed. Ash and wind-blown inorganic and organic material have been washed deep into this jumbled mass. Pocket accumulations which are sufficient for vine maple and herb establishment were analyzed however. The soil is wind borne, rich in humus, and has typical layers.

The adjoining lavas which support the *Pseudotsugeto-abietum lasiocarpae* vary little from the preceding substrate. The blocks are perhaps smaller and the larger interstices almost absent. The profile reveals both ash and scoria held in a relatively tight matrix. Subsequently, there has been no deep deposi-

tion of the finer ejectas, and the scoria is soft, crumbling easily, and subject to rapid decomposition.

The more scoriaceous gray lavas of the *Pseudotsugeto-abietum grandis* are even more soft and decomposed. The profile is a solid regolith with a finer-textured inorganic framework. The Ao layers are present and the humus zone of leaching is developed.

In the ash-lapilli flats of the *Pinetum contorti lapillosum*, mantle transmutation has been negligible underneath the existing vegetation. Substratal consolidation is evident, but does not govern opportunity for establishment, as it does in the preceding lava substrate series. Its profile has no true A_{01} layer; its surface is bare, and only scattered needles and fallen lodgepole pine constitute this layer. Humus is absent in the upper soil layer, and the parent material seems as though it has just been deposited.

For the sedge-peat intrazonal substrate of the *Carexeto-vaccinetum occidentalis*, a peat core revealed both the customary gradations, typical of bogs, from brown-fibrous peat to marl and a depth of around 15 feet in the center. The grade of the surrounding slopes and the narrow width of the marginal ditch and willow band, indicate that the edges must drop off rapidly to this depth.

Aside from the restrictions imposed by the degree of synthesized regolith available for vegetation, certain properties and their variance in the different young soils influence the character and structure of the flora that each will support. One of the most important, perhaps, is soil texture. Many associated edaphic factors affecting plants are governed by texture; and textural analysis, perhaps, defines their actions and potentialities as well as, or better than, long range measurements.

Texture affects root penetration; infiltration, rate of movement, and amounts retained of water; fertility; soil structure; soil atmosphere; and soil temperature (Daubenmire 1947). Inter-relations of these values are shown for the layers of the representative association profiles by the proportion of coarse-particle sizes, permanent wilting percentages, and sand, silt, and clay percentages (Table 17).

The few small pockets of soil available for plant growth in the block basalts of the *Aceretum circinati lavosum* have only 14 percent of their total weight of particles above 2mm. There are no sand increments and it is highest of all samples in silt content. The remaining total colloids are high also. The permanent wilting percentage of 2.00 much surpasses those of all the other soils, except those of the climax forest and it is indicative of a favorable water balance.

The most immature soil profile, the interstitial ash-lapilli of the *Pseudotsugeto-abietum lasiocarpae*, has a low percentage of coarse material (5), and about equal proportions of sand and coarse silt-sized particles. Also, there is an absence of colloidal particles. Thus water-holding capacity (pwp 0.02) and fertility are low.

The lower layers of the *Pseudotsugeto-abietum*

TABLE 17. Texture soil classes as determined by the U.S.D.A. mechanical analysis triangle, upper size class increments, and permanent wilting percentages of sampled layers of representative association profiles.

Association Profile Layers	Depth ft.	Soil Class	% over 2 mm.	P.W.P.
Pseudotsugetum taxifoliae tsugosum				
A₁	2.0	Fine Sandy Loam	15	2.80
Yellow glacial till-ash (B)	9.0	V. F. Sandy Loam	10	0.30
Aceretum circinati lavosum				
A₁	0.9	Loam	14	2.00
Pinetum contorti lapillosum				
Ash	1.0	Very Fine Sand	15	+
Lapilli	60.+	Very Fine Sand	64	+
Pseudotsugeto-abietum lasiccarpae				
Interstitial ash-lapilli	...	V. F. Sandy Loam	5	0.02
Pseudotsugeto-abietum lasiocarpae				
A₁	0.2	Fine Sandy Loam	59	1.10
Ash-lapilli-scoria	0.8	Fine Sandy Loam	79	0.05
Scoria-lapilli	1.+	Very Fine Sand	65	0.05

grandis profile composition is similar to the profile of the preceding association. However, the formation of an A_1 indicates the greater favorableness for seedling and herb establishment. Fifty-nine percent of the sample is composed of coarse material and thus aeration is greater; humus colloids are not much lower. In comparison, these combined factors indicate that less infiltration is lost by percolation, fertility is higher, and any seedling establishment has a higher potential of survival through the drier portions of the growing season than in the Douglas fir-alpine fir sere.

The ultimate mesic potential of all substrates is shown in the two sampled layers of the climax forest soil. The first layer, or the foot of A₁, contains 15 percent of coarse materials, little or no coarse sand content, and high silt and colloid content. In addition, it has the highest permanent wilting percentage (2.80) of all sampled substrates. The second layer does have a proportion of colloid increment and is mostly a single-grain coarse silt. Finally, the most coarse and least favorable substrate is that of the lodgepole pine association. The ash layer has 15 percent coarse material and lapilli stratum 64 percent. These layers have the highest percent of sand-sized particles and the lowest amounts of both silt and colloids. Correspondingly, permanent wilting percentages of the strata, as derived from the hydrometric curves, are not measurable. This is, then, an available substrate that is infertile and that has maximum infiltration, percolation, aeration, and a minimum water-holding capacity. Also, temperatures of the mantle would lag but little behind those of the atmosphere.

OTHER FACTORS

Anthropeic and animal disturbance of the vegetation is not visible. The highways through the lavas have neither disturbed nor altered the floral patterns to any appreciable extent, though many

adventives which are restricted to the roadsides have been introduced from the hay trucks that cross the pass from eastern to western Oregon during the summer. A large area of the lodgepole pine forest south of the highway junction has been cleared as an airstrip. This is kept clear of seedlings but would revert quickly once abandoned.

Evidences of fire are surprisingly absent. The old Douglas fir of the *Pseudotsugeto-abietum lasiocarpae* have fire-scarred trunks, but younger trees two or three feet in diameter have never been burned. The near replacement of Douglas fir in the climax forest suggests that in this region, fire has not altered the vegetation for quite a long time.

Western hemlock apparently requires mycorrhizal association to ecize. Seedlings occur only on dead wood, their roots covered with a yellow ectotrophic fungus. In some instances, seedlings as dense as 100 per square foot are found on half-buried logs; and they are completely absent from the nearby duff which supports lovely fir seedlings. Frequently this relationship is illustrated by lines of young western hemlock which are situated along the axis of an old log.

Cause and Effect Integration

The rather acute delineation of the separate associations, their different species complements, structures, dispositions of social organization, and their different degrees of vegetational change, as the effect, cannot be interpreted in the light of any one specific cause or environmental factor or factor group, as the cause. The factors of the "organismo-environmental complex" act collectively (Billings 1938); and the action of any one factor is qualified by the other factors and hence no one factor can be considered as being limiting for the complex as a whole (Cain 1944). Quantitative environmental data only serve to point the way to rather broad expressions of primary, secondary, and of other degrees of control of slowly interacting and changing reactions and coactions which eventually lead any vegetation to a near harmony or equilibrium in any particular sere, the climax.

Of the progressive series of linked associations adapted to the lavas, the *Aceretum circinati lavosum* is the poorest developed, the most xeric primary sere. Its unions are scattered and show neither social organization nor a semblance of dependence. Life cycles are quickly completed, and quantitative growth forms are comparatively stunted. This association is further characterized by its extreme stability, a lack of arborescent invasion, and by a high ratio of xeric to mesic adapted forms. Its area has no available formed substrate except for pockets of wind-borne material. These shallow depositions dry out early in the growing season since there is no protective consolidation, and temperature or evaporation extremes are high.

The structure and affinities of the remaining three associations the *Pseudotsugeto-abietum lasiocarpae*, the *Pseudotsugeto-abietum grandis*, and the *Pseudot-*

sugetum taxifoliae tsugosum tend, respectively, towards greater consolidation of the arborescent union and towards progressive centers of control for mesic species. In the first, the *Pseudotsugeto-abietum lasiocarpae*, social organization is loose; however, a few dominants of the Castanopsis chrysophylla union and the Chimaphila umbellata union of the *Pseudotsugeto-abietum grandis* are present. The lower strata are made up mostly of species from the *Aceretum circinati lavosum* which have lower quantitative values.

The *Pseudotsugeta-abietum grandis* is composed of the greatest species complement of all associations; its species are more mesophytic than are those of the preceding associations, and on Nash Crater, climax species have become established. Its structure shows beginnings of biotic dependency and organization. The dominants are vital and aggressive.

Certain environmental correlation seems evident. In the *Aceretum circinati lavosum*, there is no available substrate; however, there are succeeding amounts of finer material in the lavas of the following two associations. The substrate of the *Pseudotsugeto-abietum lasiocarpae* has a lower permanent wilting percentage and a lower water-holding capacity, thus is less mesic than that of the Douglas fir-grand fir association. Perhaps these factors control initiation; but then the greater consolidated structure of each association augments mesism through successive degrees of solar radiation interception, retention of the snow pack and ground storage water into the growing season, and through alteration of the substrate. In addition, the topographic features of the craters acting as reservoirs interact with the biotic and edaphic influences to form the most favorable habitat on the flows, and their slopes support, to a limited degree, regional climax species.

The most organized and mesophytic association, the *Pseudotsugetum taxifoliae tsugosum* or regional climax, is perhaps defined to the greatest extent by interspecific competition. Douglas fir, which is the most vital and represented species in all size classes in the more open *Pseudotsugeto-abietum grandis*, is unable to continue establishment; and the species with shade tolerant seedlings as western hemlock and lovely fir are replacing it. The lower strata are represented throughout the extent of the association by only a few sciophytic species which owe their existence to the amelioration of the site by the closed forest canopy. No doubt the available deep substrate accounts in part for the presence of the climax forest, but since reaction has given it its present high water-holding capacity, biotic factors overweigh edaphic. Furthermore, western hemlock depends probably upon a conditioning of the site by preceding Douglas fir forest before it can come in since such alteration is a first prerequisite for the wood fungus.

The two remaining associations, the *Carexeto-vaccinetum occidentalis* and the *Pinetum contorti lapillosum*, are primary seres with individualistic floras

quite different, separate, and syngenetically unaffiliated with the other associations.

The species of the *Carexeto-vaccinetum occidentalis* are all palustrophytes adapted to the physio-chemical conditions of the peat substrate and the high water table. These conditions likewise restrict infiltration of species from the surrounding communities. Edaphic factors are primary in this hydrosere.

The *Pinetum contorti lapillosum* has, as does the *Aceretum circinati lavosum,* scattered lower unions composed of xeric species, and in which mesic species from surrounding areas are unable to exist. The ash-lapilli substrate though deep has the lowest water-holding capacity, and permanent wilting percentage of all substrates in the area. Colloids which bind nutrient ions are absent. This sere is the most xeric and unfavorable of the seres with available substrates.

The forest canopy of the abundant and frequent single dominant, lodgepole pine, does not alter the micro-climate of the mantle since individuals of this species are short with a narrow open crown. Over most of the association, the stunted condition of the trees indicates that lodgepole pine is at its lower limits of tolerance. The plasticity of this species which permits adaptations to xeric and to other unfavorable sites, sites which are restrictive for most Northwest Pacific conifers, explains its presence on this mantle.

Dead Douglas fir seedlings are scattered throughout the lodgepole association, but this species and its associated flora are able to exist only on the small knolls of lava that rise through the ash-lapilli mantle. Such a disposition suggests that in the ash-lapilli, moisture relations are below the tolerance of Douglas fir seedlings, but that the lava affords some measure for their survival. Available water which carries the young seedlings through the dry portion of the growing season when the mantle has dried out is retained under boulders and in their pores (Haasis 1921; Turesson 1914; Robbins & Dodds, 1908).

In a final analysis the whole coniferous complex of the mid-Cascades owes its existence to the Cascadian barrier and the resulting maritime macroclimate, which is orographically modified, and to the exclusion of Polar Continental air. In the Nash Crater area, the sharp ectones, the three primary, stable seres, and the individuality of the remaining associations suggest that microedaphic control is primary because of the different substrates produced by the vulcanism which occurred perhaps between 460 to 595 years ago. Secondarily, this control is modified by forest consolidation or lack thereof which produced differences in micro-climate. Of less importance, perhaps, are localized factors such as the topographic alteration produced by the two craters, and the intense biotic influence in the climax forest.

SUMMARY

1. Phytosociologic studies were made during the summer of 1949 on several developmental communities located in the northern portion of the McKenzie

trough of the mid-Cascades in east-central Linn County, Oregon.

2. This area is comprised of a series of different, young volcanic substrates which were ejected from two parasitic vents on the lower western slope of the High Cascades. Basaltic magmas flowed west into the McKenzie trough; and in the waning stages of this vulcanism, underground differentiation produced mild explosions of ejecta which built up two symmetric, presently undissected scoria · cones, Little Nash and Nash Craters. To the lee of the craters, a deep mantle of ash and lapilli was deposited. At the westernmost penetration of the basalts, the tree ring record of a 638-year-old Douglas fir, which was surrounded by the lavas, places this volcanic interim from between 460 to 595 years ago.

3. Six associations were delineated. In each, three stands were analyzed by nested quadrats along transects for each stratum. These analyses included quantitative measurements of density, frequency, space occupied and the percent of the total, phenology, presence, and distribution of abundance of arborescent species in an arbitrary set of size classes. Edaphic and micro-climatic studies were also made for an interpretation of cause.

4. The *Aceretum circinati lavosum* association is confined to the black block basalts which have large interstices and no available substrate. Its frutescent layer, the Acer circinatum union, is dominated by vine maple *(Acer circinatum)*. The lower synusiae, as is the upper synusia, are inconsistent, their species xerophytic.

5. Four unions make up the *Pseudotsugeto-abietum lasiocarpae* association. The arboreal stratum has two dominants, Douglas fir *(Pseudotsuga taxifolia)* and alpine fir *(Abies lasiocarpa)*. The shrub, herb, and moss layers are composed of the same species as those of the vine maple association, but they have lower quantitative values. Furthermore, this association is found on block basalts which have small interstices and an available substrate.

6. The highest developmental association is the *Pseudotsugeto-abietum grandis*. It has the richest species list and the most consolidated forest cover. Douglas fir and grand fir *(Abies grandis)* dominate the upper layer, the Pseudotsugeto-abies union. Chinquapin *(Castanopsis chrysophylla)* dominates the shrub layer or Castanopsis chrysophylla union. The herbaceous layer is occupied by the Chimaphila umbellata union. The available substrate consists of a more-eroded, soft scoriaceous lava and a range of finer-textured particles.

7. These three associations show some affinities. Interchange of species mark a gradient of mesism from the *Accretum circinati lavosum,* the most xeric habitat, through to the *Pseudotsugeto-abietum grandis,* the most mesic habitat on the flows. Texture, degree of profile development, and permanent wilting percentage determinations of the substrates are closely correlated with these affinities. In the latter association and on the scoria slopes of Nash Crater where drainage supplies available moisture

late into the growing season, several species of the climax forest have come in; but their quantitative values are insufficient for them to comprise a significant component of the association.

8. On the glacial tills around the periphery of the basalts, the regional or upper montane climax forest aggregation persists as the *Pseudotsugetum taxifoliae tsugosum* association. Its upper synusia is the Pseudotsugeto-tsuga union. Its constant dominants are Douglas fir and western hemlock *(Tsuga heterophylla)*. The lower synusiae are discontinuous, only a few of their species have high vitality, and many saprophytic sciophytes are present. This is a closed forest; dependency of many species and stratal development mark it as a close-knit community. The substrate has been altered by the forest and it is deep and rich.

9. In the climax forest, Douglas firs are large and the lower size classes are lacking. Western hemlock and lovely fir *(Abies amabilis)*, as aggressive species with high reproduction and lower size class percents, are replacing Douglas fir in this highly competitive climax phytocoenosis. Syngenetic trends tie this association rather loosely with the three related developmental associations previously summarized. As reaction ameliorates principally the substrate and micro-climate, presumably, the climax would occupy these seres.

10. The two remaining associations, the *Carexeto-raccinetum occidentalis* and the *Pinetum contorti lapillosum*, are distinct primary seres of quite different species complements in which no species from surrounding associations are gaining a foothold. The former association is composed of two equally dominant species which densely cover the bog, *Carex sitchensis* and *Vaccinium occidentalis*. A Salix union forms a belt around the inner edge of the association. The species are palustrophytic, and the sere is controlled by the physio-chemical character of the peat substrate and the high water table. The latter association is comprised of an arborescent stratum of lodgepole pine, a frutescent synusia, the Ceanothus velutinus union, and a scattered herbaceous union of xerophytic herbs. The substrate is made up of loose ash-lapilli which has the lowest water-holding capacity, relative fertility, and permanent wilting percentage values of all of the available substrates.

11. The whole coniferous complex owes its existence first to the modified marine macro-climate produced by the Cascadian barrier. The abrupt ecotones, the three primary stable associations of the flows suggest that micro-edaphic control is primary. Secondarily, this control is modified by the degree of forest consolidation which produces both competitive and micro-climatic differences.

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SECONDARY SUCCESSION ON THE PIEDMONT OF NEW JERSEY

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INTRODUCTION

Near East Millstone in Somerset County, New Jersey, there exists a fairly undisturbed forest, 40 acres in extent and containing trees some of which are at least 250 years old. The forest, known as Mettler's Woods, approximates climax; at least it is a community in which vegetational change is now exceedingly slow. By referring to the vegetational and pedologic conditions of Mettler's Woods as the presumed end-points to a succession, a comparison of fields in progression to that end-point might result in a reconstruction of the secondary successional pattern of the general area.

An investigation of fields, previously cultivated but now in successive stages of natural revegetation, was therefore undertaken in 1949 and 1950 in order to determine the major changes in the vegetation and soil occurring throughout the succession. As an adjunct to the vegetational studies, the depth and density of rooting were also analyzed. The area (40° 26′ N, 74° 36′ W to 40° 30′ N, 74° 29′ W) is located in Somerset County, New Jersey, on the Brunswick formation of the Triassic shales comprising a part of the Piedmont Plateau (Kümmel 1940). Detailed studies were made of 27 fields or stands representing n'ne phases of succession.

Thanks are due to Professor Murray F. Buell, for suggesting and directing this study and to Professor Jacob S. Joffe for assistance with soils problems.

METHODS AND PROCEDURES
SELECTION OF FIELDS

Since Mettler's Woods served as a reference point for the investigation, all fields investigated had to be in the same general climatic, physiographic, and pedologic area. Thus, the fields chosen are on the Piedmont Plateau within a five-mile radius of the forest, which is located near East Millstone, Somerset County. As may be seen in Fig. 1, these fields are located to the south of the Millstone and west of the Raritan Rivers in Somerset County near the towns of East Millstone, Middlebush, South Bound Brook, Griggstown, and New Brunswick.

Inasmuch as the aim of the investigation was a reconstruction of the natural successional pattern on the Piedmont, no fields showing evidence of disturbance were chosen. Owners or their agents were questioned as to the age and treatment of each
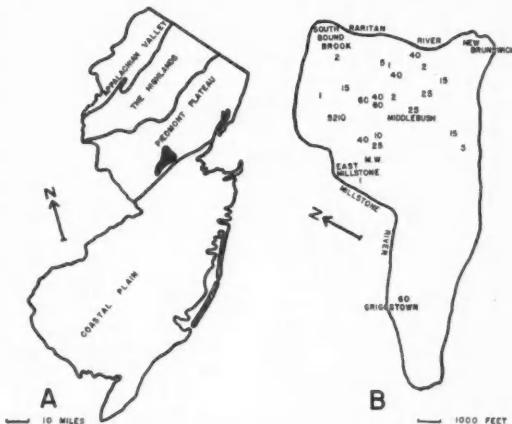
FIG. 1. A. Physiographic provinces of New Jersey, Franklin Township darkened. B. Outline map of Franklin Township, Somerset County. Investigated fields are numbered, each numeral indicating number of years since time of last cultivation. Mettler's Woods is represented by M.W.

abandoned field. Only those fields were considered for study which, following final cultivation, were left unfertilized, unburned, unmowed, and ungrazed. If these fields were on well-drained upland sites, on a soil of the Penn series closely approximating the Penn silty clay loam of Mettler's Woods, and bearing an appreciable number of red cedars, thus indicating a fire-free history, they were selected for investigation.

In all, nine age-groups are represented in the study. (The period since abandonment is designated here as the "age" of a field.) Fields abandoned 1, 2, 5, 10, 15, 25, 40, and 60 years were investigated in addition to Mettler's Woods. Since Mettler's Woods is the sole forest of its kind extant on the local Piedmont, there could be no duplication of that age-group; however, all other age-groups were studied at least in duplicate. Four fields each of the 1- and 2-year-old age-groups and three fields each of all the other age-groups (except the 10-year) were studied. There was a paucity of 10-year-old fields, and as a result only two such fields are included.

VEGETATIONAL ANALYSES

Study of the vegetation was confined to five objectives: (1) tabulation and determination of presence of all species per field; (2) frequency, density, and basal area of individual species in arborescent strata; (3) frequency and coverage of individuals in the shrub-stratum; (4) frequency and estimated coverage of individual species in herbaceous strata; and (5) an attempted forecast of the immediate future of the field by the frequency and density of the seedlings and saplings.

The methods employed for each of the above are as follows:

(1) Specimens of the vascular species of each field were collected and deposited in the Chrysler Herbarium at Rutgers University. The nomenclature employed follows that of Gray's Manual, 8th edition (1950), with the exception of an exotic not listed therein, *Ilex serrata* Thunb. Dicotyledonous herbs devoid of flowers or fruits were identified with the aid of the foliar keys of Petersen (1949). The presence of each species in an age-group was computed as the percentage of the total number of fields in that age-group.

(2) Tree-quadrats of 10x10 meters each were employed and the diameters of all trees exceeding 1 inch d.b.h. were recorded. Frequency (number of quadrats in which a species occurs expressed as a percentage of the total number of quadrats inspected), density (number of individuals per unit area), and basal area were determined from these data.

(3) A 20-meter tape was strung diagonally across and beyond each arborescent quadrat, and the cover of shrubs and trees less than 1 inch d.b.h. was measured along this transect by the line-intercept method.

(4) In each corner of the arborescent quadrat, a ½x2 meter herb-quadrat was laid from which frequency and visually-estimated coverage could be obtained. In view of the work of Bauer (1943) and Penfound (1945), the coverage value of each herbaceous and shrubby species was used as an expression of degree of dominance.

(5) The frequency and density of seedlings were determined from those appearing in the herb-quadrats. Data for saplings were obtained from a 2x10 meter strip laid down along one edge of the arborescent quadrat.

The number and kind of quadrats varied according to the age-group. No mature trees are present on fields up to and including the 10-year old fields, therefore, no tree-quadrats were employed, all herb-quadrats being laid 20 meters apart on transect lines running approximately north and south. If shrubs appeared under the transect tape, their linear coverage was recorded. In field age-groups 1-5, 50 herb-quadrats and 50 shrub-transect tapes were laid per group. In field age-group 10, 75 of each were laid. In each of the older age-groups and Mettler's Woods, 25 tree-quadrats containing 25 shrub-transect tapes, 25 sapling strips, and 100 herb-quadrats were laid. Since these older fields were of different sizes, it was difficult to apportion the number of quadrats equally among the three or four fields per age-group. Although the number of tree-quadrats per age-group always totalled 25, no field was so small that it could not accommodate 5 tree-quadrats 10 meters apart or so large that it could accommodate more than 10. In Mettler's Woods, all 25 quadrats were laid.

SOILS ANALYSES

Certain of the physical and chemical characteristics of the soils of each field age-goup were investigated. The physical characteristics determined in the field were the degree of profile development and color. Texture was determined by mechanical analysis using the Bouyoucos hydrometer-method (Bouyoucos 1936). Moisture-holding capacity was determined by the use of Hilgard cups. Structure was determined visually upon dried samples. The amount of organic matter was determined by a modification of the Tiurin method (Tiurin 1937). The following chemical characteristics were investigated: conductivity by means of the standard Kohlrausch conductivity apparatus; pH by use of a Beckman meter and also colorimetrically; exchangeable hydrogen by a modification of the Parker (1929) and Schollenberger (1927, 1930) methods; percentage of base saturation by leaching a barium-saturated soil with dilute sulfuric acid, a method employed on occasion at the Pedology Laboratory at Rutgers University; nitrates according to the method of Eastoe & Pollard (1950); and ammonia, sulfates, and chlorides qualitatively with Nessler Reagent, barium chloride, and silver nitrate quick-tests respectively.

All samples were obtained by trench cuts wherein the exposed profile could be measured as to depth and color of horizons, earthworm activity, and degree of penetration of organic matter. Four profiles per age-group were thus sampled, every horizon being sampled each time.

ROOTS

The depth of penetration and density of the roots of the dominant species in each field age-group were studied by a modification of the root-trench method employed by Scully (1942). Since only one wall of any trench was plotted, the square trench advocated by Scully was abandoned in favor of the traditional, more easily dug rectangular trench. Each trench was 1.5 m. long, 60 cm. wide, and 15 cm. deeper than the lowest observable root. This depth varied from approximately 60 to 180 cm. The face of one of the longer walls of each trench was marked off with string and nails into 8 cm squares, a total of 1.2 m thus being delimited. According to Scully's scheme, the individual squares were plotted on graph paper, various symbols being used to designate diverse diameters and species wherever possible. One root-trench was studied in each of the younger field age-groups up to and including the ten-year old, two trenches in the fifteen to sixty-year-old groups, and four in Mettler's Woods.

RESULTS

HERBACEOUS SPECIES

A list of certain of the herbaceous species occurring on the various fields is presented in Fig. 2 together with a graphic presentation of their percentages of coverage, frequency, and presence. Of the 229 species present, only two (*Potentilla simplex*, *Fragaria virginiana*) were found throughout all field age-groups, while 21 were common to all but Mettler's Woods. The majority of species appeared either in a few consecutive field age-groups or sporadically in isolated age-groups with no apparent relationship between time of abandonment and invasion. Those species never occurring in quadrats but nevertheless present on the various fields have been omitted from Fig. 2. These total 62 and are as follows, the figures in parentheses indicating the field age-groups in which each species was recorded:

Agrimonia parviflora (40, 60), *Allium* sp. (MW), *Anaphalis margaritacea* (1, 5, 10), *Anemone quinque-*

FIG. 2. (a) The coverage, frequency, and presence values (as indicated by various sized bars) of herbaceous species sampled on abandoned fields of diverse ages and in Mettler's Woods. The values for field age-groups 10 and 15 and those for 25 and 40 have been averaged. The width of each bar is an indication of the frequency, the length an indication of the coverage value of the given species, each bar being placed in one of the two columns designating presence values of more or less than 50%. For example, *Ambrosia artemisiifolia* occurred in 100% of the one-year-old fields (hence its location in the second column of field age-group one), its total frequency value for that age-group was 88% (width of bar) and its coverage value was 31.76% (length of bar). All species exhibiting estimated coverage values of 1.50% or less and frequencies of less than 20% are indicated by bars the size of that accorded *Anagallis arvensis* in the first column. An *X* indicates the occurrence of a species on the fields but not in quadrats. No presence values are indicated for Mettler's Woods since it was the sole stand of a mature forest investigated. *Andropogon scoparius* was sampled before it was mature; therefore, some *A. virginicus* probably included.

	ABANDONED		FIELDS		OF		DIVERSE		AGES				
	1		2		5		Av. of 10 & 15		Av. of 25 & 40		60		
	<50% P	>50% P	<50% P	>50% P	<50% P	>50% P	<50% P	>50% P	<50% P	>50% P	<50% P	>50% P	

LYCOPUS VIRGINICUS
LYSIMACHIA QUADRIFOLIA
MEDICAGO LUPULINA
OENOTHERA PARVIFLORA
O. PERENNIS
OXALIS CORNICULATA
O. STRICTA
PANICUM CLANDESTINUM
P. DEPAUPERATUM
P. DICHOTOMIFLORUM
P. DICHOTOMUM
P. LANUGINOSUM V. FASCICULATUM
P. LANUGINOSUM V. IMPLICATUM
P. LANUGINOSUM V. LINDHEIMERI
P. LINEARIFOLIUM
P. MERIDIONALE
P. PHILADELPHICUM
P. SPHAEROCARPON
PHLEUM PRATENSE
PHYSALIS HETEROPHYLLA
P. SUBGLABRATA
PHYTOLACCA AMERICANA
PLANTAGO LANCEOLATA
P. RUGELII
POA COMPRESSA
P. PRATENSIS
PODOPHYLLUM PELTATUM
POLYGALA VERTICILLATA
POLYGONATUM BIFLORUM
POLYGONUM HYDROPIPEROIDES
P. PERSICARIA
P. TENUE
POTENTILLA NORVEGICA
P. RECTA
P. SIMPLEX
PRUNELLA VULGARIS
PYCNANTHEMUM VIRGINIANUM
RANUNCULUS ABORTIVUS
RUDBECKIA HIRTA
RUMEX ACETOSELLA
SETARIA GLAUCA
SMILACINA RACEMOSA
SOLANUM CAROLINENSE
SOLIDAGO ALTISSIMA
S. CANADENSIS
S. GIGANTEA V. LEIOPHYLLA
S. GRAMINIFOLIA
S. HISPIDA
S. JUNCEA
S. NEMORALIS
S. PUBERULA
S. RUGOSA
SPIRANTHES CERNUA
TRICHOSTEMA DICHOTOMUM
TRIFOLIUM AGRARIUM
T. ARVENSE
T. HYBRIDUM
T. PRATENSE
T. REPENS
VERBASCUM BLATTARIA
VERNONIA NOVEBORACENSIS
VIOLA LANCEOLATA

SPACE   39.52%   40.30%   27.92%   37.31%   43.80%   60.2%   91.0%

FIG. 2. (b): continuation of Fig. 2a.

folia (MW), *Anthemis arvensis* (1, 2), *Anthoxanthum odoratum* (1, 2, 5), *Asclepias tuberosa* (2), *Aster puniceus* (2), *A. schreberi* (MW), *Barbarea vulgaris* (5), *Bidens laevis* (40), *Carex laxiflora* v. *gracillima* (MW), *C. radiata* (MW), *C. setacea* (2), *Carex* sp. (15), *Cassia fasciculata* (10), *Chenopodium album* (MW), *Cichorim intybus* (2), *Cirsium pumilum* (1), *C. vulgaris* (2, 5, 10, 40), *Claytonia virginica* (MW), *Commelina virginica* (40), *Desmodium nudiflorum* (MW), *Echium vulgare* (1), *Erigeron annuus* (10), *Euphorbia vermiculata* (2), *Festuca obtusa* (MW), *Galinsoga parviflora* (2), *Galium pilosum* (MW), *Glyceria striata* (MW), *Heuchera americana* (MW), *Hieracium scabrum* (10), *Hypericum canadense* (5), *H. mutilum* (1, 2), *Juncus effusus* (1), *Lappula echinata* (2), *Leersia virginica* (MW), *Lepidium densiflorum* (1), *Lespedeza capitata* (60), *Lotus corniculatus* (25), *Luzula multiflora* (MW), *Lycopodium tristachyum* (60), *Melilotus officinalis* (2), *Monotropa uniflora* (MW), *Oenothera biennis* (25), *O. fruticosa* (40), *Osmorhiza claytoni* (MW), *Paronychia canadensis* (MW), *Poa annua* (2), *Polygala sanguinea* (5, 10, 40), *Polygonum hydropiper* (MW), *P. pensylvanicum* (2, 10), *Ranunculus recurvatus* (MW), *Saxifraga virginiensis* (MW), *Solidago uliginosa* (2), *S. uliginosa* v. *linoides* (MW), *Stachys tenuifolia* v. *platyphylla* (40), *Taraxacum officinale* (1), *Triodia flava* (40), *Verbascum thapsus* (2), *Viola affinis* (MW), and *Viola papilionacea* (MW).

Similarly, species which occurred in but one field age-group, if their estimated coverage was less than 0.10% are omitted. These in turn total 28 and are as follows:

Amphicarpa bracteata (MW), *Anemonella thalictroides* (MW), *Artemisia tridentata* (25), *Asclepias quadrifolia* (MW), *Botrychium virginianum* (MW), *Carex cephalophora* (MW), *Cerastium vulgatum* (5), *Danthonia sericea* (25), *Galium aparine* (MW), *G. triflorum* (MW), *Geranium maculatum* (MW), *Geum canadense* (MW), *Hibiscus trionum* (60), *Maianthemum canadense* (MW), *Panicum boscii* (1), *P. latifolium*

(60), *Pilea pumila* (MW), *Polygonum convolvulus* (1), *Raphanus raphanistrum* (1), *Rumex crispus* (1), *Sanicula canadensis* (MW), *Symplocarpus foetidus* (MW), *Tiarella cordifolia* (MW), *Uvularia perfoliata* (MW), *U. sessilifolia* (MW), *Viola latiuscula* (60), *V. sagittata* (40), and *Viola* sp. (MW).

The remaining 139 species are listed in Fig. 2, the various bars representing the average coverage, frequency, and presence value of each species in the diverse field age-groups. The values for field age-groups 10 and 15 and those for 25 and 40 were averaged to reduce the size of the figure.

The various species ranged in coverage from considerably less than 1% to almost 32%. The coverage values in Fig. 2 must be interpreted cautiously. They are estimates which have been averaged, hence in themselves representing values ranging from much above or below the mean to slight deviations from it. Since they are not absolute values they show only trends of dominancy. These trends may appear more or less decisive depending on the variations of coverage and frequency of given species in the several fields of any field age-group. Although certain of the trends may be obliterated by resorting to a consideration of averages only, it may thus be shown that the invasion and ecesis even of the dominant species is not as consistent on the Piedmont of New Jersey as described for the Piedmont of North Carolina (Oosting 1942).

Soon after cultivation of a field is halted, a weedy flora invades the field. The one-year-old fields support a great growth of ragweed (*Ambrosia artemisiifolia*) towards the end of the summer, and it is this species which appears to be dominant in absolute

coverage, but if one were to consider the growing season as a whole, evening primrose *(Oenothera parviflora)* would dominate. The latter loses all importance after the first year, and though it and other evening primroses appear spottily in older fields, the genus never regains its original dominance. *Rumex acetosella* and *Agrostis hyemalis* are consistently high in newly abandoned fields, the former maintaining its coverage as long as a quarter-century later, the latter dwindling after a decade. Of the ninety-four species found in the one-year-old fields (Table 1), twenty-six were annuals: an approximate one-fourth of the total species. This proportion would be increased somewhat if one were to consider the coverage of all the annuals in relation to the total coverage of all species sampled within the quadrats (Table 2). It is evident that almost one-third of the one-year-old fields is covered with therophytes, half of these annuals being common to the younger fields only, the others maintaining their coverage or appearing sporadically in the older fields. With the exception of *Solidago juncea* (which attained more than 2% coverage on the two-year-old fields, and therefore may be present on some newly abandoned fields), all the herbaceous perennials later assuming dominancy are present in the one-year-old fields. While a striking decrease in therophytes is noted both floristically (Table 1) and in dominance (Table 2) from the youngest to the oldest fields, there is not the preponderance of annuals often noted in newly-abandoned fields (Oosting 1942). Despite the high degree of colonization noted, almost 40% of the area of the one-year-old fields was untenanted by herbs. Although it may have supported lichens or seedlings, this area was devoid of herbaceous growth and as such was recorded as "space" in the herb layers (Fig. 2).

An additional feature to be noted is the relatively large proportion of species non-indigenous to eastern North America (Table 3). Almost 29% of the

TABLE 1. Life-form spectra (in percent) of all species present on abandoned fields of diverse ages and in Mettler's Woods. Figures in parentheses indicate plants which are juvenile or immature specimens of species which at maturity are in the given life-form. Life-form categories follow those assigned by Ennis (1928).

Age	Total	P	MP	mP	N	Ch	H	G	Th
1......	94	0	(3.2)	(4.3)	0	0	53.2	11.7	27.6
2......	104	(1.0)	(3.8)	(5.8)	1.0	0	53.8	11.5	23.1
5......	95	(2.1)	(8.4)	(10.5)	2.1	2.1	49.5	8.4	16.9
10......	91	(2.2)	(9.9)	(8.8)	0	2.2	51.6	4.4	20.9
15......	96	(5.2)	(15.6)	(9.4)	2.1	2.1	47.9	7.3	10.4
25......	104	(3.8)	(9.5)	13.5	1.0	2.9	48.1	10.6	10.6
40......	122	(5.7)	(10.8)	13.1	2.5	1.6	42.6	9.8	13.9
60......	104	(7.7)	(13.5)	10.6	2.9	1.9	42.3	8.6	12.5
M W......	115	15.7	13.9	13.9	2.6	0.9	30.4	15.6	7.0

P — Megaphanerophytes: Tall trees over 30 m. in height.
MP — Mesophanerophytes: Trees 8-30 m. in height.
mP — Microphanerophytes: Low trees 2-8 m. in height.
N — Nanophanerophytes: Shrubs under 2 m. in height but over 25 cm. tall.
Ch — Chamaephytes: Low shrubs with buds borne less than 25 cm. above surface.
H — Hemicryptophytes: Herbs with perennating bud at surface; often covered by debris.
G — Geophytes: Herbs with perennating bud buried in soil.
Th — Therophytes: Annuals.

TABLE 2. Life-form spectra based on list of species present in quadrats on abandoned fields of diverse ages and in Mettler's Woods (upper figures) and spectra based on their coverage values (lower figures), the latter in percentage. The percentages of the spectra based on cover represent the percentage that each life-form contributes to the total coverage contributed by all life-forms. Figures in parentheses indicate plants which are juvenile or immature specimens of species which at maturity are in the given life-form. For explanation of symbols, see Table 1.

Age	Total	P	MP	mP	N	Ch	H	G	Th
1........	73	0	(2)	(3)	0	0	38	9	21
		0	0.31	0.28	0	0	65.59	2.12	31.69
2........	72	(1)	(4)	(1)	0	0	41	10	15
		0.01	0.23	1.21	0	0	78.11	5.42	15.01
5........	63	(1)	(4)	(2)	1	2	36	6	11
		0.06	0.97	0.45	0.15	0.19	91.97	0.77	5.43
10........	68	(2)	(8)	(7)	0	1	37	3	10
		0.67	1.20	1.54	0	1.03	86.65	1.70	7.20
15........	75	(2)	(10)	(4)	1	2	41	7	8
		0.11	6.49	6.83	0.89	0.77	80.45	2.87	1.58
25........	79	(4)	(6)	8	1	3	41	9	7
		0.86	10.21	5.51	0.65	0.81	79.49	1.13	2.33
40........	87	(5)	(10)	10	1	1	40	9	11
		0.67	20.15	9.23	0.14	1.35	63.78	3.33	1.34
60........	76	(6)	13	8	1	1	32	5	10
		2.52	58.49	9.12	0.05	0.06	27.17	1.15	1.44
M W.....	50	8	5	6	2	1	12	13	3
		55.24	30.28	0.53	12.01	0.01	0.19	1.60	0.14

TABLE 3. Number and percentage of non-indigenous species (following Gray's Manual. 8th ed.) on abandoned fields of diverse ages and in Mettler's Woods.

Age of Field	Non-Indigenes	Total Species	% Non-Indigenes
1........	27	94	28.72
2........	33	104	31.73
5........	21	95	22.11
10........	12	91	13.19
15........	17	96	17.71
25........	21	104	20.19
40........	21	122	17.21
60........	16	104	15.38
M W......	5	115	4.35

species are not native, this percentage decreasing measurably with length of abandonment.

The two-year-old fields differ from the one-year-old fields in the higher coverage and frequency of goldenrods and other perennials, and a decrease in the annual coverage (Fig. 2, Table 2). Goldenrods (especially *Solidago nemoralis*) contribute most to the aspect of the fields, but *Daucus carota* and *Potentilla simplex* are fairly important also. Unlike the above species, with coverage values exceeding 10%, the majority of the species exhibit values below 2%. Some of these, like *Anagallis arvensis* and *Verbascum blattaria* are restricted to fairly recently aban-

doned fields, while others, like *Achillea millefolium* and *Acalypha virginica*, exhibiting fair frequency but low cover, appear in all fields from the youngest to the oldest despite a diminution in frequency and cover. Another difference in the two-year-old fields lies in the successional nature of the dominant species: there is no rapid decline or extinction of these species following the second year of abandonment as there is in the case of the dominants of the one-year-old fields. Indeed, a two-year-old field may often be best marked by the abundance of dead Oenothera stalks. The area unoccupied by herbs remains essentially unchanged.

The five-year-old fields maintain high goldenrod coverage and in addition exhibit much *Aster ericoides*. This species attains a 2% coverage in one-year-old fields, more than doubles it in two-year-old fields, and exhibits a 15% coverage in the five-year-old fields. An ubiquitous hawkweed, *Hieracium florentinum*, also present throughout the succession, is quite noticeable at this stage. *Potentilla simplex* and *Daucus carota* are still extensive. *Andropogon scoparius*, although present throughout the succession, becomes appreciable within five years of abandonment and maintains varyingly high coverage thereafter. The percentage of therophytes has dropped to almost 17, the coverage of 11 annuals on quadrats equalling 5.43% of total coverage (Tables 1 & 2). The percentage of non-indigenes has also decreased (Table 3). Only 28% of the herb layer is space, this being the lowest recorded, and indicates the greatest herbaceous colonization. As woody colonization increases, herb coverage decreases with a concomitant increase in the space of the herb layer.

The herbaceous aspect of the ten-year-old fields is decidedly a Solidago-Andropogon one with a strong admixture of *Aster ericoides* and *Hieracium florentinum*. Of all age-groups studied, the ten-year-old fields exhibit the greatest growth of goldenrods, especially *Solidago nemoralis* and *S. graminifolia*. Towards late autumn, the broomsedges (*Andropogon scoparius* and *A. virginicus*) actually appear more conspicuous than they were at the time of sampling (late summer). *Potentilla simplex* and *Erigeron strigosus* are somewhat less important than *Aster ericoides* and *Hieracium florentinum* but still noteworthy. A second hawkweed, *H. scabrum*, appears on the drier stretches of one field. The slight increase in therophytes (Table 1) is occasioned by the invasion of a few annuals common to older fields, e.g., *Crotallaria sagittalis*. Similarly, the slight increase in coverage of annual species (Table 2) may result from the increase of *Erigeron strigosus*. Non-indigenes have decreased to about 13% of the species present (Table 3). The increase in woody species to be noted later is responsible for the increase of total space devoid of herbaceous cover, from 27.92% in five-year-old fields to 32.09% in ten-year-old fields.

Lichen coverage, heretofore negligible, is quite extensive. No data were assembled regarding the frequency and coverage values of lichens, but the species encountered in the various age-groups are listed in Table 4.

TABLE 4. Floristic analysis of lichens present on abandoned fields of diverse ages. Identifications by Dr. John W. Thomson, Jr. of the University of Wisconsin.

Species	ABANDONED FIELDS						
	2	5	10	15	25	40	60
Cladonia sp.	*						
C. atlantica Evans f. *squamosissima* Evans						*	
C. capitata (Michaux) Spreng. f. *imbricata* (Nyl.) Evans		*					
C. chlorophaea (Floerke) Spreng.							*
f. *carpophora* (Floerke) Anders						*	
f. *pseudotrachyna* Harn.				*			
f. *pteryaota* (Floerke) Vainio					*		
f. *simplex* (Hoffm.) Arn.				*		*	
C. coniocraea (Floerke) Spreng. f. *ceratodes* (Floerke) Dalla Torre & Sarnth.		*					
C. cristatella Tuck.				*			*
f. *squamosissima* Robbins							*
f. *vestita* Tuck.			*	*	*	*	
C. fimbriata (L.) Fr.			*		*		
C. macilenta Hoffm. f. *styracella* (Ach.) Vainio						*	
C. mateocyatha Robbins							*
C. subcariosa Nyl.			*		*		
f. *evoluta* Vainio				*	*	*	*
f. *squamulosa* Robbins					*		

Fields abandoned for fifteen years differ slightly in their herbaceous aspect from the ten-year-old fields because of the increase of Andropogon and the reduction of *Solidago nemoralis* and *S. graminifolia*. Despite this, the goldenrods collectively maintain a higher coverage value than the broomsedges, and appear to be dominant. Moreover, two other goldenrods increase in coverage; these are *S. juncea* and *S. rugosa*. *Hieracium florentinum* is more than equivalent in coverage to the Andropogons, but its flattened rosette belies its dominance in comparison to the taller, robust broomsedges. *Potentilla simplex* has a comparatively high coverage value, as does *Fragaria virginiana*, the two species which are present from the one-year-old fields to the forest itself. *Danthonia spicata* attains a fair coverage. The number of annuals is low, and their coverage is even lower (Tables 1 & 2). The non-indigenes have increased somewhat, but this is in large part the result of the entrance of woody forms at a rapid rate. Total space unoccupied by herbs equals more than 42%.

The twenty-five-year-old fields exhibit less goldenrod coverage than fifteen-year-old fields, despite an increase in *Solidago juncea*. *Aster ericoides* is the most conspicuous single dominant. *Hieracium florentinum* is almost as important as the aster, but of course rarely seems so. The Andropogons form only a frac-

tion of their former (and seemingly subsequent!) coverage; this obtained on the three fields studied. An explanation of the significance of this highly perverse situation will be attempted later. *Rumex acetosella* would appear to rank beneath Aster and *Hieracium florentinum* in coverage value, but an abnormally high (23%) value for one field distorted the average, considering the 1% each exhibited in the other fields. *Fragaria virginiana, Danthonia spicata,* and *Potentilla simplex* are widespread, and *Linaria vulgaris* attains its highest frequency on these fields. The number of therophytes (Table 1) is not too different from those present on the fifteen-year-old fields, but their coverage is slightly higher (Table 2). A slight increase in non-indigenous species is noted (Table 3), still the result of invading woody species. The total space unoccupied by herbs is almost 43%.

The forty-year-old fields are characterized by Andropogons with appreciable admixtures of the goldenrods, especially *Solidago juncea. Fragaria virginiana* and *Danthonia spicata* are important subdominants. Of the species contributing less to total coverage, *Apocynum cannabinum* and *Antennaria neodioica* reach their peaks here both as to frequency and coverage. Woodland species begin to enter the succession: e.g., *Smilacina racemosa* is noted for the first time. The lichen cover is extensive and rich in species (Table 4). Although the therophyte flora appears high (Table 1), the coverage is low (Table 2). Non-indigenous species are gradually decreasing in number (Table 3), a resumption of the trend broken slightly in the fifteenth to twenty-fifth years following abandonment. Area unoccupied by herbs in the forty-year old fields averaged 48.21%.

The oldest fields of the study had been abandoned for approximately sixty years. The total cover of herbs was only about 40%. The dominant species are *Solidago juncea* and the Andropogons. *Solidago nemoralis, Rumex acetosella,* and *Danthonia spicata* are sub-dominant, but the decrease in cover is not the only factor which distinguishes these fields herbaceously from the younger sites. *Smilacina racemosa* and *Galium circaezans,* species in the oak-hickory forest, are found in the more mesic nooks of these fields. *Hieracium florentinum* and *Aster ericoides* contribute little to total coverage. *Fragaria virginiana* is still quite evident. Therophytes are low in total number and rather low in coverage (Tables 1 & 2). The non-indigenous species comprise only about 15% of the total species, a decided decrease since the beginning of the succession (Table 3).

In Mettler's Woods, as the growing season progresses, the herbaceous vegetation is gradually reduced from an earlier maximum coverage to approximately 10% of the total area of soil available for colonization, yet despite this, 57 species maintain themselves on the forest floor. While never rich in species in comparison to younger fields, the herbaceous flora is greatest towards late summer, although total coverage is greatest in mid-spring prior to leaf-unfolding of the trees with attendant closing of the

forest canopy. The quadrat data were obtained in early June at a time when *Podophyllum peltatum*
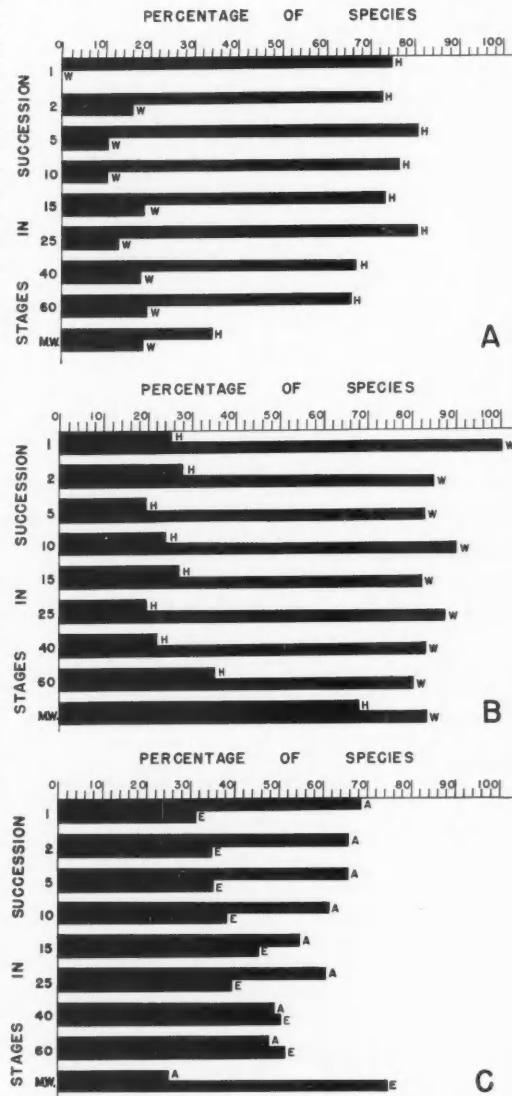

FIG. 3. Percentage of herbs, woody species and total flora disseminated by wind or animals (Ridley 1930) on abandoned fields and in Mettler's Woods.

A. Percentage of herbaceous (H) and woody (W) species of each field age-group whose seeds or fruits are dispersed by the wind.

B. Percentage of herbaceous (H) and woody (W) species of each field age-group whose seeds or fruits are dispersed by birds, animals, or insects either epi- or endozoically.

C. Percentage of all the species (herbaceous and woody) of each field age-group whose seeds or fruits are disseminated by the wind (A) or by birds, animals, or insects (E).

exhibited slightly more than 3% coverage, a reduction of its previous status. The only other species at this time with more than 1% coverage is *Circaea quadrisulcata*. The majority of the species, like *Smilacina racemosa*, *Impatiens capensis*, and *Polygonatum biflorum* exhibit approximately 0.5% or less coverage (Fig. 2). Both the coverage and frequency values of these woodland species are much inferior to those of the younger fields. The annuals are the lowest, both in number and percentage cover, in comparison to all fields studied (Tables 1 & 2); the non-indigenes are similarly lowest in number (Table 3).

The variation in mode of dissemination of the plants occupying the diverse fields is presented graphically in Fig. 3. The herbaceous species bear fruits or seeds which are largely disseminated by wind in the early years of abandonment. Towards the climax, the population shifts and a flora dispersed mainly epizoically and endozoically occupies the fields.

WOODY SPECIES

Ninety-one woody species were found growing on the various fields. Of these 91, only two, *Prunus serotina* and *Rhus radicans* are present throughout the succession. Three more species, *Myrica pensylvanica*, *Rhus glabra*, and *Rubus flagellaris* occur on all the abandoned fields but not in Mettler's Woods.

The other eighty-six species are variously disposed throughout the age-groups.

The coverage, frequency, and presence values of certain of the woody species occurring in the shrub layers of the various fields is shown in Fig. 4, the values for field age-groups 10 and 15 and those for 25 and 40 having been averaged. Species (39) present on the fields but not in quadrats or under line-transects, have been omitted from Fig. 4. These are here enumerated together with the field age-groups (in parentheses) in which each was recorded:

Acer ginnala (40), *A. saccharinum* (15, 60), *Amelanchier canadensis* (15, MW), *Berberis thunbergii* (MW), *B. vulgaris* (MW), *Betula nigra* (60), *Carpinus caroliniana* (MW), *Carya cordiformis* (60, MW), *C. glabra* (MW), *C. ovalis* (MW), *C. ovata* (MW), *Catalpa bignonioides* (5), *Chimaphila maculata* (MW), *Crataegus mollis* (MW), *C. pruinosa* (15), *C. intricata v. straminea* (5, 25, 40), *Ilex serrata* (MW), *Juglans nigra* (MW), *Lindera benzoin* (25, MW), *Liriodendron tulipifera* (MW), *Maclura pomifera* (1), *Ostrya virginiana* (MW), *Platanus occidentalis* (40), *Populus grandidentata* (40), *Quercus bicolor* (60, MW), *Q. coccinea* (15, MW), *Q. velutina* (40, MW), *Rhus copallina* (5, 25, 40, 60), *R. typhina* (2, 40), *Rosa canina* (40), *Rubus occidentalis* (MW), *R. ostryifolius* (MW), *Sambucus canadensis* (2, 10, MW), *Smilax pulverulenta* (MW), *Spiraea tomentosa* (2, 5), *Tilia americana* (MW), *Vaccinium stamineum* (MW), *Vitis cinerea* (25), *V. labrusca* (15).

The one-year-old fields have a meager, mostly unnoticed population of shrubs. Less than 2% of the
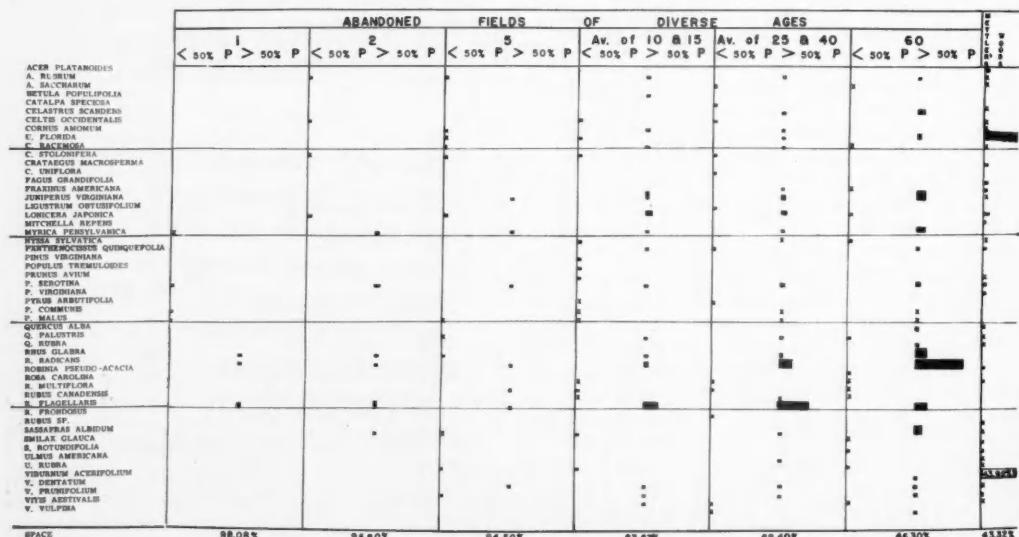
FIG. 4. The coverage, frequency, and presence values (as indicated by various sized bars) of woody species sampled in the shrub layers of abandoned fields of diverse ages and in Mettler's Woods. The values for field age-groups 10 and 15 and those for 25 and 40 have been averaged. The width of each bar is an indication of the frequency, the length an indication of the estimated coverage value of the given species, each bar being placed in one of the two columns designating the presence values of more or less than 50%. For example, *Rhus radicans* had presence and frequency values of 100% (width of bar) each and an estimated coverage value of 26.80% (length of bar) in field age-group 60. All species exhibiting estimated coverage values of 1.50% or less and frequencies of less than 20% are indicated by bars the size of that accorded *Acer rubrum* in field age-group 2. An X indicates the occurrence of a species on the fields but not in quadrats. No presence values are indicated for Mettler's Woods since it was the sole stand of a mature forest investigated.

TABLE 5. The density (D, in field age-groups 1-5, individuals per 50 sq. m.; in 10-year-old fields, individuals per 75 sq. m; and remaining field age-groups, individuals per 100 sq. m.), frequency (F), and presence (P), of arborescent seedlings encountered on abandoned fields of diverse ages and in Mettler's Woods.

Species	1			2			5			10			15			25			40			60			M W	
	D	F	P	D	F	P	D	F	P	D	F	P	D	F	P	D	F	P	D	F	P	D	F	P	D	F
Acer rubrum				1- 2-25						1-13 -100			1-1-100			3-2-100						10- 6- 66			5- 4	
Carya sp.																									9- 4	
Cornus florida																			3-3-100			14- 3- 66			168-61	
Fraxinus americana																									3- 3	
Juniperus virginiana							5-8-100			2-2.6-100			5-4-100			10-8-100			11-8-100			39-21-100			2- 2	
Prunus serotina	47-22-25			7-10-50			5-4-100			1-1.3-100			1-1-100			4-2-100			8-6-100			11- 9-100			2- 2	
Pyrus communis	1- 2-25															1-1- 66						1- 1- 33				
Quercus alba																						1- 1- 66			3- 3	
Q. palustris													1-1-100													
Q. rubra																						5- 5- 66				
Q. velutina																									2- 2	
Sassafras albidum							1-2- 33												23-9- 50			89-35-100				
Ulmus sp.													1-1-100													

area of the fields is covered with shrubs, seedlings or vines, about 98% of the soil surface being un-occupied by these plants. Despite low coverage values, *Rubus flagellaris*, *Rhus glabra*, and *R. radicans* are established here and largely remain throughout the succession (Fig. 4). If a source of seed is good, seedlings of *Prunus serotina* for example, are more numerous one year after abandonment of a field than subsequently (Table 5). It will be seen, however, that their mortality rate is quite high.

Two-year-old fields show a reduction both in shrub coverage (Fig. 4) and seedling density (Table 5) of *Prunus serotina*. Increased coverage of *Rubus flagellaris* and *Rhus radicans* is noted together with the successful invasion of an ubiquitous non-indigene, *Lonicera japonica*. *Myrica pensylvanica* provides greater coverage than the previous year and *Acer rubrum* first appears. The appearance of two-year-old fields is nevertheless distinguished from one-year-old fields not so much by the minor increase in shrubs but by alterations in the herbaceous flora. Total area unoccupied by shrubby growth equals about 95%.

Quite soon after abandonment, the species that especially lends character to the succession, *Juniperus virginiana*, becomes established. Several factors affect the time of eccesis, the most notable, of course, being source of seed and presence of seed-ingesting birds. The three five-year-old fields all had young red cedars, some at least two years of age. Although the four one-year- and the four two-year-old fields were all bordered by red cedar hedgerows, and there is by no means a dearth of birds feeding on red cedar in the vicinity, careful scrutiny within the fields revealed no seedlings. Investigation of a three-year-old field and a four-year-old field also proved disappointing. Nevertheless, it would appear from the presence of the two-year-old plants in the five-year-old fields, that Juniperus may enter the succession within the first five years, probably the second or third year after abandonment. *Cornus florida* also appears early but its seedlings are so scattered that they are not encountered in quadrats until later in the succession.

The change in physiognomy at the time represented by the five-year-old fields is due entirely to the woody species, now beginning to appear above the herbs (Fig. 5). The young red cedars are most striking, though often no more than half a meter tall, and contributing on the average a coverage value of much less than 1% (Fig. 4). By virtue of its spreading habit, *Myrica pensylvanica* contributes more to coverage but is approximately equal in frequency. The dogwoods *(Cornus amomum, C. florida, C. racemosa, C. stolonifera)* and the Viburnums *(V. dentatum, V. prunifolium)* occur, though not necessarily on the same field. One seedling of *Sassafras albidum* was noted, but seedlings of Juniperus and *Prunus serotina* were more numerous (Table 5). The greater growth of shrubs and the invasion of newer woody species further decreased the amount of space unoccupied by them to about 94%.

By the tenth year of abandonment (Fig. 6), the red cedars have grown another half to three-quarters of a meter, and increased to a frequency of 93%, but their coverage is only slightly higher than that obtaining for the five-year-old fields. *Rubus flagellaris* forms a dense growth in local areas, while *Myrica pensylvanica* maintains an over-all coverage of ap-

FIG. 5. Young *Juniperus virginiana* (0.5 m tall) in field abandoned 5.5 years previously. A clump of *Andropogon scoparius* is visible behind the red cedar.

proximately 1%. The dogwoods increase somewhat, and they and *Acer rubrum* appear as saplings about one meter in height. The number of seedlings of all species is low (Table 5). Space unoccupied by shrubs and immature arborescent forms equals about 93%.

Fig. 6. Field abandoned about 10 years previously. Juniperus, 1 m tall, and other young trees of *Acer rubrum* and *Cornus florida* are evident. Andropogon is common in this field.

The fifteen-year-old fields assume an open-park aspect, for the taller red cedars are about 2.5 meters high, and the numerous young saplings of *Pyrus malus*, *Acer rubrum*, and *Ulmus rubra*, although not quite as tall, emphasize the increasing number of woody species (Fig. 7). Juniperus totals about 1% coverage and is the dominant tree, but the shrubs cover more ground. *Rubus flagellaris*, for example, attains a coverage value exceeding 14%, and *Rhus radicans*, which has been increasing steadily since abandonment exhibits about 4% coverage. A great growth of *Lonicera japonica* on one field distorted the average coverage of that species. Seedlings are still few in number (Table 5). The density of saplings is greatest for Juniperus (Table 6). On two of the three fifteen-year-old fields, a number of scrub pines *(Pinus virginiana)* appear to be successful. Although usually confined to succession on sandier

Fig. 7. Field abandoned about 15 years previously. Trees of Juniperus are 2-2.5 m tall, those of *Pyrus communis* somewhat taller, and bushes of *Viburnum prunifolium* are evident.

soils, they occasionally occur on the Triassic shales. The extent of woody growth is such that the amount of soil surface not covered by shrubs or saplings equals about 74%.

TABLE 6. The density (D, number of individuals per 500 sq. m.), frequency (F), and presence (P) of saplings and shrubs encountered on abandoned fields of diverse ages and in Mettler's Woods.

Species	15			25			40			60			M W	
	D	F	P	D	F	P	D	F	P	D	F	P	D	F
Acer rubrum	1-	4-	33	2-	8-	66	2-	8-	50	10-16-	66		8-20	
A. saccharinum	1-	4-	33											
Amelanchier canadensis	1-	4-	33											
Cornus florida				1-	4-	33				2-	8-	66	123-92	
C. racemosa	1-	4-	33	5-	4-	33				2-	4-	23		
C. stolonifera				8	4-	33								
Fagus grandifolia													3-12	
Fraxinus americana													22-32	
Juniperus virginiana	17-48-100			19-64-100			59-64-100			90-96-100				
Pinus virginiana	4-12-	33												
Populus grandidentata							1-	4-	25					
Prunus serotina				3-12-	66		4-16-	75		3-12-	33		1- 4	
Pyrus arbutifolia	2-	4-	33											
P. malus							1-	4-	25					
Quercus palustris				1-	4-	33	2-	8-	50					
Q. rubra										19-32-	66			
Rhus glabra	9-16-	66		13-20-	66		13-16-	50		70-68-100				
Rosa carolina										1-	4-	33		
Sassafras albidum							14-20-	50		70-60-100				
Ulmus rubra	1-	4-	33	7-20-	66					1-	4-	33	2- 4	
Viburnum dentatum										1-	4-	33		
V. prunifolium										7-	4-	33		

Fields abandoned for twenty-five years exhibit red cedars of more than 1 inch d.b.h., and numerous other species. The cover of smaller plants of Juniperus in the shrub layer is still low, but *Prunus serotina* and *Sassafras albidum* have begun to increase. *Rhus radicans* maintains its inexorable trend of increase as *Rubus flagellaris* reaches its peak. Space unoccupied by shrubs and immature trees has dropped to 64%. The number of seedlings of Juniperus is somewhat in excess of the younger fields but it is still not appreciable (Table 5). Seedlings of *Prunus serotina* and *Acer rubrum* have also increased. An increase in the density of saplings is observed in the case of most species, especially Juniperus and *Rhus glabra*. *Cornus stolonifera* and *Ulmus rubra* are also well represented by saplings (Table 6). More than 79% of the total woody basal area is contributed by Juniperus, although this only totals 1.22 square feet on the basis of 2,500 square meters. *Quercus palustris* contributes 6.55% and *Ulmus rubra* and *Acer rubrum* contribute approximately 5% each to the total woody basal area (Table 7).

As is expected, the forty-year-old fields have a richer and more extensive shrub cover in addition to a more varied supply of taller trees (Fig. 8). Space unoccupied by shrubby growth is about 61%. Juniperus is still the most important arborescent species, but cover of its smaller trees has increased to only 2%. *Sassafras albidum*, among the arborescent species, is next in contribution to cover in the shrub layer. Of the vines and lower shrubs,

TABLE 7. The basal area (B.A.) in square feet, density (D, per 2500 sq. m.), and frequency (F) of trees over 1 inch d.b.h. encountered on abandoned fields of diverse ages and in Mettler's Woods.

Species	25				40				60				M. W.			
	B.A.	% B.A.	D	F	B.A.	% B.A.	D	F	B.A.	% B.A.	D	F	B.A.	% B.A.	D	F
Acer ginnala...............					0.006-	0.20-	1-	4								
A. rubrum................	0.081-	5.27-	6-	12	0.051-	1.59-	5-	8	0.715-	5.37-	24-	28	0.320-	0.50-	2-	8
A. saccharum............													0.013-	0.02-	1-	4
Betula nigra.............									0.067-	0.50-	1-	4				
Carya ovalis.............													6.850-	9.80-	3-	12
Cornus florida...........	0.012-	0.80-	1-	4	0.126-	3.90-	9-	16	0.928-	6.97-	30-	48	13.900-	19.00-	331-	100
Fagus grandifolia........													4.370-	6.80-	10-	12
Fraxinus americana.......					0.031-	0.95-	2-	4	0.096-	0.72-	1-	4	0.005-	0.01-	1-	4
Juniperus virginiana......	1.220-	79.52-	59-	84	2.349-	72.40-	62-	80	8.352-	62.70-	232-	96				
Nyssa sylvatica..........									0.056-	0.42-	1-	4				
Ostrya virginiana.........													0.005-	0.01-	1-	4
Prunus serotina..........					0.062-	1.91-	3-	8	1.129-	8.48-	31-	52				
Pyrus communis..........	0.039-	2.56-	4-	16					0.083-	0.62-	3-	8				
P. malus................									0.026-	0.20-	3-	4				
Quercus alba............													30.540-	43.80-	18-	52
Q. palustris.............	0.101-	6.55-	1-	4	0.153-	4.72-	1-	4								
Q. rubra................									0.400-	2.98-	5-	12	7.900-	11.30-	4-	16
Q. velutina..............													6.200-	8.90-	4-	16
Sassafras albidum........					0.465-	14.33-	20-	12	1.471-	11.04-	52-	60				
Ulmus rubra.............	0.082-	5.30-	6-	12									0.005-	0.01-	1-	4

FIG. 8. Field abandoned about 40 years. Note the gradual closing of the Juniperus stand and the trees of *Prunus serotina* and *Sassafras albidum*.

Rubus flagellaris, although decreasing, still has a coverage of about 17%. *Rhus radicans* is very widespread, covering as it does 8% of the total sampled area. Of seedlings, Sassafras are the most common. Those of Juniperus are more abundant than in the preceding age-field (Table 5). There are more than four times the number of saplings of Juniperus on the 2,500 square meters sampled than any other species (Table 6). Saplings of Sassafras and shrubs of *Rhus glabra* are quite common, while saplings of *Prunus serotina* are more evident than previously. Juniperus contributes 72.4% of the total basal area of wood. The total basal area of Sassafras equals 0.46 square feet, or 14.33% of the total woody basal area (Table 7). The basal area of *Quercus palustris* has increased from that of the twenty-five-year level, but the percentage has decreased. An exotic maple,

Acer ginnala, has invaded one of the forty-year-old fields from a neighboring landscaped estate, and it contributes 0.20% to the total woody basal area. This field also supports a specimen of *Ligustrum obtusifolium* which came from the same source.

The oldest (60-yr.) abandoned fields resemble young groves. Forty-six percent of the area is unoccupied by shrubby growth, thus approximately half the fields support some type of vine, shrub, or immature tree. Coverage figures cannot adequately convey a picture of the almost impenetrable thickets formed by this extensive growth. Growth of red cedar is at its peak in this age-group: trees of 10 inches d.b.h. and more than 5 m. tall are not uncommon (Fig. 9). Despite this, young trees cover only about 4% of the shrub layer (Fig. 4). *Sassafras albidum* contributes 3% and *Prunus serotina* contributes less than 3% to the total coverage of species in the shrub layer. But it is the vines and creeping shrubs running rampant over the fields which impart an aspect totally different from the other fields. The species which slowly and steadily increases its minute coverage from the time of initial abandonment until its dominance in the sixty-year-old fields is, of course, *Rhus radicans* which has now attained a coverage of almost 30%, largely as festoons on the red cedar trees. *Rubus flagellaris*, *Rhus glabra*, *Myrica pensylvanica*, and *Celastrus scandens*, collectively covering almost 21% of the area, also produce an effect of untrammeled growth. While never very high in coverage value, the truly mesic species characteristic of woodlands gradually supercede the long-established species and remain even when the mature forest develops. These species are *Cornus florida*, *Prunus serotina*, *Quercus alba*, *Q. rubra*, *Viburnum acerifolium*, *V. dentatum*, and *V. prunifolium*, all but the second exhibiting

FIG. 9. Field abandoned 60 years previously as seen from an adjacent field. Mature trees of Juniperus form a fairly closed stand.

FIG. 10. Mettler's Woods as seen from an adjacent field. Note the marked stratification produced by the shorter trees, especially *Cornus florida*. Some of the tallest oaks and hickories are 24 m in height.

coverage values approximating 0.50% at this time.

The sixty-year-old fields have an abundance of seedlings, Sassafras being most numerous. Juniperus seedlings are abundant, too, but the presence of those of *Cornus florida*, *Quercus alba*, and *Q. rubra* has more significance despite their lesser numbers (Table 5), because these are the species important in the mature forest. Saplings of Juniperus and Sassafras contribute much to the high sapling-count, the highest noted in all the field age-groups studied. The density of the saplings of *Quercus rubra* and *Acer rubrum* is significant in that the former is higher than that displayed in Mettler's Woods, and the latter is approximately equivalent to the value in the mature forest (Table 6).

Regarding the mature trees, red cedar contributes 62.70% of the total basal area, or approximately eight square feet (Table 7). Sassafras, *Prunus serotina*, *Cornus florida*, and *Acer rubrum* are next in importance. *Quercus rubra* contributes almost 3%. The stage is thus set for the gradual transition towards the oak-hickory forest.

It is unfortunate that there was no stage transitional between the sixty-year-old fields and the mature forest. We may refer to Mettler's Woods as an example of the nearest approximation of a local climax forest (Fig. 10). The forest itself is imposing in the height and size of its dominant trees. Certain problems regarding its status may be noted from an examination of the data but these will be left for subsequent discussion. Shrubs and transgressives (young trees) occupy slightly more area than they do in the sixty-year-old fields, about 43% of the area being devoid of them. The dominant shrub is *Viburnum acerifolium* (almost 44%); the dominant transgressive is *Cornus florida* (cover, about 23%), the former also exhibiting slightly higher frequency than the latter. *Lonicera japonica* is next in importance but very low in coverage (about 2%), and another vine, *Rhus radicans*, has decreased to but a fraction of its former coverage (much less than 1%). The saplings of common trees, like *Prunus serotina*, *Fraxinus americana*, and *Acer rubrum* contribute very little to total coverage, but some, like *Cornus*

florida (density, 125) and *Fraxinus americana* (density, 22), appear rather dense. Saplings of the dominant trees, *Quercus alba*, *Q. ruba*, and the species of *Carya* were observed in the forest but never found in the quadrats (Table 6). There are some seedlings of *Quercus alba* (but none in quadrats) and *Q. velutina*, but the predominant seedlings are those of *Cornus florida* (density, 168, Table 5). Seedlings of species of *Carya* were noted on the forest floor, but none appeared in the 100 square meters sampled.

The dominants are clearly indicated when considering their basal area (Table 7). *Quercus alba* contributes almost 44% to the total woody basal area. *Cornus florida* is sub-dominant with a value of 19%. *Quercus rubra* and *Q. velutina* each contributes at least 9%. *Carya ovalis* and *Fagus grandifolia*, although their basal area is low, exhibit higher percentages of frequency than any other sub-dominant.

There is little variation in the mode of dissemination of the woody forms throughout the succession (Fig. 3); regardless of the time since abandonment, approximately 84% of the woody species bear fruits or seeds dispersed by birds and animals. However, if the flora is taken as a whole, the overwhelming number of herbs in the younger fields shifts the general trend to an approximation of the herbaceous trend; *i.e.* a general decrease in wind-disseminated species and an attendant increase in faunal-disseminated species.

SOILS

The fields under investigation are located on the Brunswick formation (Kümmel 1940) of the Triassic shales which grade into soil materials of the Penn series, mostly Penn silty clay loam (U.S.D.A. Soil Survey of the Trenton Area 1926). The outstanding characteristic of this soil is the reddish color imparted to it by the slowly-weathering ferrous aluminum shales which are for the most part the result of sedimentation in quiet Triassic waters. Lack of disturbance during sedimentation produced heavy (but occasionally sandy) shale beds rather

homogeneous as to particle size and mineral composition, this homogeneity to-day being reflected in the fairly uniform textural classes noted in the various horizons of the soil. These soils belong to the group of clay rocks made up of clay and clay-like minerals in association with iron and aluminum sesquioxides and other minerals in smaller quantities.

Although existing in the broad climatic belt conducive to a type of podzolization which would normally produce a brown podzolic soil, the soil must be classified as an endodynamomorphic body now largely resisting further weathering of its mineralogical fractions. The latter, having undergone considerable weathering prior to and during the Trias, bear few constituents capable of further chemical weathering. As Joffe (1937) states, "The fact that Fe, Al, and other constituents show very small differentials in the profile of the Penn silt loam . . . indicates no movement of them in the profile. And yet the B horizon is in its physical appearance typical of an illuviation horizon: it has a compact constitution. This simply means that the more highly dispersed particles are a resultant of physical disintegration with no change in composition." The small particle size, the masking presence of the red color, and the paucity of other minerals produce a nondescript, rather shallow soil material largely lacking in horizon-differentiation. This material may in time be endowed with the characteristics of a brown podzol, but must to-day be classified as an immature soil.

The typical profile is rarely more than half a meter in depth, and often less, for shale is frequently encountered within 60 cm of the surface. A layer of humus, often no more than 2 cm thick, is found in the forest and the older fields. In Mettler's Woods, this layer approximates the type designated as medium mull by Heiberg & Chandler (1941). A gradation in color, accentuated upon drying, may be noted from one horizon to the next. The Ap is often a cocoa-brown, the B a pale, rusty brown, and the C a rusty brown. Structure varies from crumbly to nutty, with a reduction in the size of the crumb-aggregates noted towards the C. A mild type of granulation is observed where the parent material contains lenses of sandstone embedded with the shale. Earthworms were noted in most of the soils especially in the B horizon.

The soil of Mettler's Woods will be discussed with reference to the properties analyzed, and then a brief review of the results of analyses of the younger fields will be presented. It is perhaps best to state at the outset that, with minor exceptions, differences between the age-groups may more often be ascribed to textural differences than to varying times of abandonment.

The soil in Mettler's Woods is more readily differentiated into horizons than that of cultivated fields, but even here the reddish color prevents facile visual identification. Textural differences of the horizon are more readily noted by insertion of a sharp trowel. A certain amount of clay settles in the B horizon during weathering, thus insuring a fairly light-textured A horizon. The A_1 is rendered even lighter by the autumnal accumulation and subsequent incorporation of organic matter. The relatively high content of organic matter in the A_1 (3.18%) is largely responsible for the high moisture-holding capacity (62.09%) for that horizon, the highest noted. The electrolytes, especially in the A_1, are high; even the nitrates, ammonia, sulfates, and chlorides appear appreciable at times. The average total exchange capacity (18.79 m.e.) is lower than that obtaining in the sixty-year-old fields (23.73 m.e.), but it represents a wider range.

The soil profiles of the younger fields are for the most part shallower than in the mature forest. Minor textural differences are to be found between the soils of the younger fields, these differences being reflected in the variations in the moisture-holding capacity and exchange capacity of the several horizons. No marked increase in the percentage of organic matter is noted with an increase in time of abandonment. Where differences in amount of organic matter do occur, they may be attributed to the degree of aeration which may vary according to the clay content. Little change is to be observed in the pH of these younger fields: the relatively high pH (6.0—6.6) of the one-year-old fields may be ascribed to the residual effects of the lime and fertilizer applied during the previous growing season, and the slightly low pH (5.4—6.0) of the soil in the five-year-old fields may be attributed to the unusual abundance of granitic pebbles, remnants of pre-Wisconsin glaciation. No discernible trends may be noted in the content of electrolytes as a whole (viz. conductivity) or sulfates in particular but fluctuations in nitrates, ammonia, and chlorides do occur. It would appear that fluctuations in exchangeable hydrogen probably result from differences in soil texture up to the forty-year level, after which minor increases occur owing to a greater annual accumulation of litter.

Roots

The density and depth of penetration of the roots of plants dispersed throughout the various abandoned fields are presented in Table 8. Each datum represents the density of the roots of various sized classes in an area 0.18 square meters (an area 1.2 m wide and 15 cm deep).

The depth of penetration of the roots as a whole appears to vary with the age of abandonment, from 60 cm in the younger fields to 1.8 m in Mettler's Woods. Fragments of shale, if not consolidated beds, are often encountered within 60 cm of the surface. The number of roots penetrating the shale increases with the age of abandonment, e.g. the roots of Quercus alba descend through almost a meter and a half of shale in Mettler's Woods. On the whole, the penetration of the shale is accompanied by a simultaneous decrease in the density of the smallest roots and an increase in the larger ones.

The greatest density of roots is observed in the

TABLE 8. The depth of penetration and density (per 0.18 sq. m.) of roots of plants encountered on abandoned fields of diverse ages and in Mettler's Woods.

Depth in cm.	Diameter in mm.	1*	2*	5*	10*	15*	25*	40*	60*	M W
0-15	< -1	990	568	868	923	867.5	1223.0	1000.5	828.0	290.5
	2-9	13	2		3	8.5	19.5	10.0	20.5	54.5
	10 or >						0.5		2.5	3.5
15-30	< -1	368	85	192	99	400.5	495.0	405.0	297.0	155.5
	2-9			3		1.5	4.0	6.5	9.5	29.3
	10 or >								1.5	3.3
30-45	< -1	57	43	133	63	160.0†	267.0†	186.5	133.5	115.5
	2-9	1				0.5	2.0		3.0	15.5
	10 or >									5.5
45-60	< -1	20†	7†	19†	18†	110.0†	71.5†	68.0	47.5†	86.3†
	2-9						1.5		0.5	9.7
	10 or >									
60-75	< -1		4†	2†	1†	14.0†	8.5†	9.5†	34.0†	85.0†
	2-9						0.5		0.5	6.6
	10 or >									
75-90	< -1					1.0†	2.0†	7.0†	9.0†	92.0†
	2-9								0.5	8.0
	10 or >									
90-105	< -1							0.5†	0.5†	29.3†
	2-9									4.3
	10 or >									
105-120	< -1									21.3†
	2-9									1.0
	10 or >									
120-135	< -1									2.0†
	2-9									
	10 or >									
135-150	< -1									3.6†‡
	2-9									2.3
	10 or >									
150-165	< -1									
	2-9									
	10 or >									
165-180	< -1									1.6†
	2-9									0.6
	10 or >									

*Years since time of last cultivation.
†Shale encountered.
‡Lens of hard clay encountered locally.

upper 15 cm of the soil, the vast majority of these being small roots less than 1 mm. in diameter. A decrease in the density of the smallest roots is noted towards the oldest fields, but the variations in the younger fields are insignificant if one considers that only one root-trench was studied in each. Furthermore, in age-groups five to sixty, each trench was dug about a meter away from one of the dominant specimens of *Juniperus virginiana.* If tufts of *Andropogon* happened to be in the vicinity, the density of the roots would be measurably increased. Owing to the high percentage of *Hieracium florentinum*, the greatest density of roots appears in the twenty-five-year-old age-group. There ensues a gradual, if interrupted, increase in the density of the larger roots

after the second year of abandonment; the one-year old fields exhibit a somewhat greater number of these roots owing to the extensive coverage of *Rumex acetosella.* Very large roots, however, are not noted until twenty-five years after abandonment.

From 15-30 cm below the surface, the total density of roots is less than one-third of the number observed in the first fifteen centimeters. Here, too, the greatest density was encountered in the fields abandoned for twenty-five years. The decrease in the density from the first to the second 15-cm layer is of lesser magnitude in Mettler's Woods than elsewhere.

The total density of roots drops even further in the layer 30-45 cm below the surface. The twenty-five-year old fields maintain their superiority in density. Mettler's Woods, still exhibiting a lower density of small roots than that obtaining in the younger fields, maintains its superiority in numbers of larger roots.

As the roots penetrate successively deeper layers, their total density decreases, but a relative increase in density is noted with increases in age of abandonment in the case of roots of all sizes. Below 90 cm, the density of roots in Mettler's Woods rapidly declines.

DISCUSSION

TRENDS—VEGETATION

The successional trends displayed on the Piedmont of New Jersey are somewhat comparable to those observed on the southern half of the Piedmont (Crafton & Wells 1934; Billings 1938; Coile 1940; Oosting 1942) or in southern New England (Lutz 1928). Floristic composition varies from site to site, but the maintenance of certain dominants throughout the general area affords good comparison.

Fields abandoned one year are frequently dominated by ragweed *(Ambrosia artemisiifolia)* in New Jersey as well as in North Carolina (Keever 1950). Keever's results show that ragweed dominance is a product of the type of cultivation and the previous crop. In North Carolina, it may also be a dominant the second year after abandonment (Oosting 1942). Where evening primrose *(Oenothera parriflora)* is so common in one-year-old fields of New Jersey, horseweed *(Leptilon canadense)* is the dominant in North Carolina (Oosting 1942; Keever 1950); but in both regions these rapidly lose importance and are replaced by species of *Aster, Solidago,* and *Andropogon.*

A comparison of the degree of dominancy of these herbaceous species in the two sections of the Piedmont is impossible because the methods of field study are not comparable. The dominants of older fields are all present in newly-abandoned fields in New Jersey, while in North Carolina, their entrance may be delayed at least a year (Keever 1950). This does not in anyway hasten the succession in New Jersey; it is rather a reflection of a different climate and a resultant of the larger number of species encountered (94 in New Jersey; 35 in North Carolina as reported by Oosting 1942).

The greater variety of species on the northern Piedmont would also account for local variations in some fields from the general aster-goldenrod-broomsedge dominancy, as in the case of the occasional dominance of *Daucus carota, Potentilla simplex, Hieracium florentinum,* or *Fragaria virginiana* (Fig. 2). These deviations rarely occur over a long period, but are soon replaced by one or another of the dominant triumvirate. Occasionally, a species is present but with very low coverage in a field where one would expect it to be dominant, considering the general trend. Specifically, the rarity of Andropogon in the three widely-separated fields abandoned for twenty-five years is not symptomatic of a great reduction from the fifteen-year level, attended later by a great increase to the forty-year level. It may rather be an indicator of a poor seed-year, or a series of poor seed-years for Androgogon when these three isolated fields were newly abandoned, or some factor preventing seedling-survival. As Piemeisel (1951) states, "Destruction of a future dominant, a selective destruction, need not involve any great quantity of vegetable matter if it is at a critical time in the series."

The essential difference in the dominant herbs of the two investigated areas of the Piedmont is not in degree but in time of dominancy. Aster remains one of the dominants for a longer period, and the two dominant species of Solidago are of greater importance in New Jersey than farther south, especially in the older fields. Goldenrod dominancy in older fields has also been reported in New England (Lutz 1928).

As for the herbaceous flora as a whole, annuals are far less important here than elsewhere. In North Carolina, Oosting (1942) discovered that 57% of the species on fields abandoned one year were therophytes. In New Jersey, this number is only 28%, and even a consideration of the total coverage value of these plants reveals that less than 32% of the average one-year old field is occupied by annuals.

Despite the greater number of species, the fewer annuals, and the floristic differences in dominants, succession on the Piedmont moves with the same velocity in New Jersey as in North Carolina. The indicator species of the sub-climax, whether red cedar in the North or pines in the South, invade young fields within a few years after abandonment, and by the fifth year, appear above the herbs. Seedlings of the climax species, especially of bird-disseminated species, are established almost immediately after abandonment. Many of these succumb in competition for light and soil-status to the more vigorous herbs, but a certain number prevail and eventually attain maturity. Cherries and dogwoods are most successful, and by the sixtieth year, oaks and a few hickories are apparent in the understory. Although no field abandoned for longer than 60 years was investigated in New Jersey, Lutz (1928) reports a stand of 60-year-old red cedars in New England which had begun to deteriorate. It would appear that approximately 100 years is required for the first

oaks and hickories to attain dominancy on the Piedmont of New Jersey, an equivalent period being reported by Billings (1938) in North Carolina.

With the approach to the status of the climax community, the floristic differences between areas become more pronounced. New Jersey represents an area transitional to the hemlock-hardwood forests to the North in New York and New England (Lutz 1928) and the southern oak-hickory forests with their occasional components of pine (Oosting 1942). Hemlock is not found in Mettler's Woods, but is located in cool ravines and north slopes of central New Jersey. Fewer sugar maples and beeches are found in the forests on the Piedmont of New Jersey than are common to the North; on the other hand, there is a richer proportion of oaks and hickories more reminiscent of the South.

But beyond arborescent species, differences are most noted in the ground vegetation. A few of the species may be found in forests from North Carolina to New England, but more are limited to either the South or the North. Cain (1950) states that a high proportion of geophytes in a flora is associated with a brief growing season such as might occur in a desert or that fraction of the growing season prior to post-vernal closing of the canopy in a forest. The higher percentage of geophytes (16%, Table 1) in Mettler's Woods than in oak-hickory forests of North Carolina (Oosting 1942) suggests a generally low level of light in the former. Is it possible that this is related to a general increase in the opening of the forest canopy as one proceeds from New England to the southern Piedmont, and that this variation may largely be responsible for floristic and ecological variations in the herbaceous populations?

The presence in the mature oak-hickory forest of fewer non-indigenous species than in the successional stages (Table 3) would argue for an interpretation of the oak-hickory forest, as represented by Mettler's Woods, as a closed community. It is impossible for the alien species to compete successfully with the long-established native vegetation.

TRENDS—SOILS

A summation of the analyses of certain physical and chemical properties of the soils investigated in the present study does indicate a lack of decisive correlation between any property and the age of abandonment. Where differences occur, they are more readily attributed to minor differences in the percentages of silt and clay present than to other factors. If a single abandoned field were examined over a period of 60 years, a slight amelioration in the surface might be observed in the moisture-holding capacity, exchange capacity, percentage of base saturation, and electrolytic content, all reflections of a gradual accumulation of organic matter.

Billings (1938) noted a striking change in the first 2 inches of the soil on the southern Piedmont. This improvement of the soil was due to the effects of the vegetation during the period of the succession: the copious deposit of pine needles which accumulated

annually appeared to be a primary factor in the alteration of the soil. While this layer of the first two inches of soil was not sampled independently in the present study, it was included in a surface sample of approximately 15 cm; thus, any variation in the top few centimeters would be minimized in a consideration of the entire Ap horizon. The results thus represent an average of the Ap horizon. Since the seedlings of woody species present in the succession on the northern Piedmont are all equipped with long tap roots—unlike the shortleaf pines studied by Billings on the southern Piedmont—there is little value to be obtained in shallow sampling. Billings found no changes occurring in the soil beneath the surface 2 inches. Below this 2-inch layer, the differences between fields of varying ages apparently are related to differences in soil texture, an equivalent condition obtaining in New Jersey.

Another southern Piedmont study (Coile 1940) is similar in scope to Billings', but directed instead at loblolly pine succession. Coile concluded: "Physical characteristics of soil measured as volume-weight, water-holding capacity, and air-space change but little during succession and are not related in a causal manner to succession." Neither are changes in the chemical properties of the soil responsible for the entrance of the pines or the oaks. Instead, Coile attributes to time and chance the establishment of the woody forms. His interpretation of the relationships between squirrels and the size and location of the abandoned field will be reviewed later.

It would appear that red cedar succession on Penn soils is similar to loblolly succession on the Piedmont in North Carolina (Coile 1940) in that any minor changes of the soil accruing with abandonment other than accumulation of surface litter and its attendant phenomena (Billings 1938), are to be regarded more as the result than the cause of any particular succession.

TRENDS—ROOTS

The greater density of the smallest roots in the uppermost horizons of the soil and the increased density of the larger roots towards the lower horizons noted in the present study have often been observed (Billings 1938; Scully 1942).

The general depth of penetration of the roots increases with the age of abandonment of a field, a reflection of the increased percentage of woody species in the flora. Variations in the total density of roots are more dependent on the nature of the species present than the comparative texture of these soils, since lateral roots tend to be short in fine-textured soils (Anderson & Cheyney 1934). There is, however, a pronounced decrease in the density of the smallest roots of the uppermost horizon of Mettler's Woods. This decrease is due to the fewer numbers of herbaceous species in the forest.

Differences in the rooting habits of the dominant arborescent species are not such as to account for the successional pattern. Red cedar and oak seedlings both exhibit tap roots, and their growth require-

ments as far as soils are concerned appear to be similar. A study of root development on three soil types carried out in the Duke forest on a number of arborescent species including white oak and red cedar indicated an inverse relationship between available soil moisture and root growth of their seedlings (Duncan 1941). Both white oak and red cedar seedlings exhibited the best root growth on soils possessing a high air capacity, low porosity, and a small amount of available moisture.

It is very possible that the rooting habits of the dominant herbaceous species are responsible for their successional pattern insofar as competition for soil moisture may be of prime importance during droughts. Experimentation with these plants under different conditions of light and on varied soil textures would no doubt uncover relationships relative to the succession.

ASPECTS OF SUCCESSION

In 1916, Clements listed six stages in succession: nudation, migration, ecesis, competition, stabilization, and reaction. Nudation involves the removal of the soil, a condition important in a consideration of primary succession. However, nudation of a field may be interpreted as including only the removal of vegetation: this is the aspect of nudation involved in secondary succession. Migration of plants is effected by various means, thereby providing for invasion of plants upon an area. Ecesis entails establishment, and competition involves ". . . a struggle between individuals for growing space, both above and below ground, and for light, water, and nutrients" (Toumey & Korstian 1937, p. 156).

Each stage is, of course, completely interrelated with the others. However, if each is considered individually in an interpretation of secondary succession on the Piedmont of New Jersey, certain ecological features of this succession may be noted.

NUDATION

In secondary succession, nudation is never complete, and the extent of nudation determines the pattern of the succession. Even where the soil is plowed in preparation for planting and then abruptly abandoned prior to seeding, there does not exist a situation of true nudation. Embeded in the soil are countless seeds from previous growing seasons, and a large percentage of them is capable of germination. The pattern of a secondary succession has been reviewed in this report. Successions may vary with the degree of nudation (Dansereau 1946), but this study has been concerned only with those situations where land has been cultivated and then left idle as cultivation ceased.

MIGRATION

Migration *per se* has little meaning without a consideration of ecesis and competition, but for the moment, these latter will be omitted. The time of migration may precede by several years the actual initiation of the succession. It would be interesting to determine what percentage of the plants inhabiting a

one-year-old field resulted from germination of viable seeds lodged in the soil for several preceding years. Chepil (1946) reported viability in seeds of the following species (present in the succession in New Jersey) deposited in the soil for five years: *Chenopodium album, Lepidium densiflorum, Medicago lupulina,* and *Taraxacum officinale.* However, the probability of seeds germinating very many years after deposition is unlikely. Oosting & Humphreys (1940) collected soil from successive stages in North Carolina and observed that germination tests ". . . show a succession of species, as do the plants above ground, and, in general, they are indicative of the same succession."

Where actual invasion occurs, assuming ample source of seed in each case, it would appear that the youngest fields are inhabited by herbaceous species whose fruits and seeds are largely dispersed by the wind, an inwards progression from hedgerows being noted. Not a small percentage of these wind-disseminated forms (Ridley 1930) are also transported epizoically in mud adhering to the fur and feathers of campestral birds and animals.

Dissemination of the woody species is largely effected endozoically as the succession proceeds towards the climax (Fig. 3). The smaller a field and the greater its proximity to a woodlot, the sooner will woodland species enter the succession (Coile 1940). Squirrels and other nut-caching rodents do not often venture into open fields, but minor sorties around the outskirts of forests may provide for peripheral invasion. Where fields are quite removed from local woodlots, invasion may perhaps be traced to the activity of crows and other birds, the same birds which effect dissemination of red cedar. That germination of seeds is often enhanced after ingestion by certain birds and mammals has been experimentally demonstrated by Krefting & Roe (1949).

It is evident that there is no set time in the succession that the arborescent forms first appear. Invasion and subsequent ecesis of red cedars and species dominant in later stages of the succession, like cherry, dogwood, or red maple, occur quite soon after abandonment, and if oaks and hickories are delayed until a grove is established, it may be ascribed to the reluctance of squirrels and chipmunks to traverse open fields.

ECESIS

Whatever the mode of entrance may be, the ability of a plant to become established depends on its inherent limits of tolerance and the degree to which these limits are exceeded by neighboring species, i.e. competition. It is common to consider annuals as more aggressive colonizers than are perennials during the early stages of abandonment. The life-cycle of annuals is abbreviated, hence a rapid foliation and flowering provide for a larger plant than that of a juvenile perennial often elaborating a rhizome of one sort or another. The second year of abandonment witnesses a closing of the underground network of the rhizomes and roots of the perennials to the exclusion of the annuals. Another example of the difficulty of establishment is the following. As the succession continues, bare patches of soil appear between the clumps of Andropogon. These patches are underlain immediately below the surface by the widely ramifying fibrous roots of the grass. As a result, the soil between the clumps is unoccupied except for shallow-rooting rosettes like hawkweeds (*Hieracium* spp.) or closely investing lichens. The inability of seedlings to penetate a lichen mat, or, once germinated, to withstand injury by the hygroscopically sensitive, heaving mat has been reported by Allen (1929).

The factors affecting the establishment of seedlings on mineral soil have received considerable attention. Much of this attention has centered about the so-called limiting factor for growth of climax species. Toumey (1926), in a report of his famous trenching experiments, indicated that soil moisture was often the factor limiting the growth of seedlings. Aaltonen (1926) observed that the poorer the site, the greater the light requirement; and recently, Shirley (1945), reviewing the subject, stressed the importance of assessing the interrelationship between light and other factors, but concluded that light is probably the most important factor affecting growth after the light intensity has been reduced to 20% of full sunlight.

If a discussion on the ecesis of seedlings is confined to red cedar and oak, several questions arise immediately:

1) Why does red cedar become established earlier than oak?

2) Does red cedar contribute to the ecesis of oak?

3) Why does red cedar fail to establish itself under oak?

Although no experimental evidence is available, certain conjectural statements may be proffered regarding these questions. The invasion of red cedar prior to that of oak has been demonstrated. Although a few seedlings of oaks appear early in the succession, the only oak exhibiting ecesis within five years after abandonment is pin oak (Fig. 4), a member of the late stage of the succession, occasionally present in the wetter parts of Mettler's Woods. (The presence of pin oak in the young fields of the vicinity does not necessarily suggest that these fields exhibit poor drainage. While Gray's Manual states that *Quercus palustris* is a species inhabiting swampy woods and bottoms at low altitudes (p. 546), in central New Jersey it occupies a much wider range of habitat. For example, in addition to its occurrence in young, abandoned fields on upland sites, it is often found on the dry bluffs above the Raritan River.)

Within fifteen years after abandonment, the more consistently mesic oaks appear, and by the sixtieth year, a few are often members of the understory. The reason that red cedar becomes established earlier in the succession than the oaks is obviously because of its greater ease of invasion. Since a number of

oaks do become established fairly early in the succession, putative deficiencies or excesses of certain environmental factors may not be responsible for lack of establishment. More probably, it is the source and mode of transfer of seed discussed above which limits the number of oaks appearing in younger fields. Although saplings of oaks are found in all fields abandoned for more than five years (Fig. 4), the seedlings were so scattered that there were never more than five noted in 100 sq m of any one field age-group (Table 5). The above discussion of chronology has therefore been based on field experience coupled with data of the sapling population.

Does red cedar contribute to the ecesis of oak? According to the concept of succession at first outlined by Clements, one stage in succession actually paves the way for the succeeding stage by altering the environment in such a way as to make it unfavorable for itself but favorable for the newer stage. An example of this has been nicely demonstrated on the southern Piedmont in the case of shortleaf (Billings 1938) and loblolly pine (Coile 1940). In both cases, the annual accumulation of pine needles produces a thick, hygroscopic mat of litter rather impenetrable to the short roots of pine seedlings. Oak seedlings, equipped with taproots sometimes twice the length of the shoot, easily descend through the mat and are able to tap the mineral soil below. The pine seedlings suffer extinction presumably through desiccation (Billings 1938) or starvation (Kozlowski 1949).

Such a situation does not obtain on the northern Piedmont. The accumulation of litter never exceeds a fine, crumbly mat about two centimeters thick, since red cedar and dogwood leaves, for example, are fairly rich in calcium (Coile 1933; Chandler 1939; Bard 1946) and are readily digested by the earthworms present throughout the succession. Although a slight increase in the moisture-holding capacity of the Ap horizon is noted after a few years of abandonment, this level is sustained with little change until after the oaks are established, when a second, mild increase occurs. No other edaphic factor varies appreciably throughout the sere, and therefore, one is again tempted to consider the maturing red cedar stand merely as a lure to woodland rodents. It is probable that any stand of trees, whether red cedar, sassafras, dogwood, or pin oak, would provide enough shelter for such animals, and thus acorns would be brought into the field.

A second supposition, advanced by Shirley (1945) is that pioneer woody species such as red cedar rarely cast shade dense enough to preclude invasion of other species, but their shade and root competition may markedly reduce the growth of all but the most tolerant species. Lutz (1928) considers that ". . . the shade of red cedar . . . is so slight that it has little if any detrimental influence on the growth of the young hardwoods; in fact it may be beneficial to them during juvenile growth since it lowers soil temperature and evaporation." The ability of oak

seedlings to maintain growth at very low light intensities has been demonstrated experimentally by Gia (1927) and more recently by Kozlowski (1949).

Thus it would appear that red cedars or any pioneer trees may aid in the establishment of oak by (1) forming a grove providing shelter for rodents and their introduction of acorns; (2) providing shade which restricts competition from exacting heliophiles ("sunlovers"); and (3) providing a reduction in soil temperature and evaporation.

Why does red cedar fail to establish itself under oak? Since red cedar is known to grow in a variety of habitats ranging from stream banks to exposed bluffs (Oosting 1942), it apparently exhibits a very wide tolerance to extremes in the supply of soil moisture. As has been stated previously, the moisture-holding capacity of the surface soil may perhaps increase after the oaks are mature, and thus if there is no drought, there is obviously no dearth of water. Even if intense competition for water should occur from actively growing oak trees, there is neither a morphological or ecological deterrent to the growth of red cedar, since the seedlings exhibit fine tap roots and the tree is known to be unusually resistant to drought (Stiles & Melchers 1935; Albertson & Weaver 1945). It would seem that red cedar probably fails to establish itself under oak because of the intense shade cast by the latter. Experimentation such as that performed on pine and oak by Kozlowski (1949), designed to determine the photosynthetic rate and output of a species under varying amounts of soil moisture, is essential for an elucidation of the reasons red cedar fails to establish itself under oak.

COMPETITION

Competition is an all-inclusive term embracing features of migration, ecesis, reaction, and stabilization, and often employed when the specific factors responsible for a given situation are unknown or poorly understood. Competition may be inter- or intraspecific, but ecological techniques and knowledge are such that the effects of interspecific competition on succession have just begun to be investigated (Keever 1950; Piemeisel 1951).

As Keever (1950) has demonstrated, the forces of competition may be elucidated if the life-cycles and tolerances of the organisms investigated are clearly understood. None of the three species she studied in North Carolina, *Leptilon canadense, Aster pilosus*, and *Andropogon virginicus*, is present as a dominant on the Piedmont of New Jersey, but the latter two have ecological equivalents here: *Aster ericoides* and *Andropogon scoparius*. If it may be assumed that their life-cycles and tolerances are similar to those of their counterparts, the differences between their interrelationships in New Jersey and North Carolina may be briefly outlined.

At the time of abandonment at the close of the growing season, seeds of all subsequent herbaceous dominants are already present or brought into the field by the various agents of dissemination. Eve-

ning primrose—like horseweeds in North Carolina—germinates at the end of the growing season, winters as a rosette, and produces a tall, vigorous floral shoot the following summer. It may produce another rosette the following winter. Ragweed, a summer annual, is most abundant towards the end of the growing season. Since horseweed is not present, aster cannot be stunted by decay products of its roots and tops. What, then, delays aster for a few years on the northern Piedmont? Aster, germinating in the spring, matures in the late summer and autumn. Keever has demonstrated that *Aster pilosus* makes its best growth with abundant light and water. It is therefore possible that the taller evening primroses and ragweed shade the young northern asters and inhibit their maximum growth. Shading or inhibition continues for a few years until aster becomes the dominant species in approximately the fifth year rather than the second as in North Carolina. Exactly why it is delayed for such a long period is unknown. It nevertheless does maintain high coverage for twenty years, but is eventually repressed by the more drought-resistant broomsedge (Keever 1950), for there is generally an inverse relationship between the coverage values of the two species; in other words, when the coverage of one is high, the coverage of the other is low.

Again unlike the situation in North Carolina, Andropogon does not assume dominancy the third year of abandonment but around the fifteenth. Although it is able to compete successfully with less drought-resistant species, it requires full light (Keever 1950). Its long delay may probably be ascribed to effects of the very successful goldenrod, *Solidago nemoralis*. Why the latter should rapidly lose dominance after the tenth year is unknown, but that broomsedge quickly fills the breach is doubtless significant.

The relationships between the dominant herbaceous species and the invading woody forms is at present only dimly comprehended, and it is to investigations similar in scope to that of Keever's which one must look for aid in explaining the progression of plants during succession.

REACTION

In succession on the Piedmont of New Jersey, there is no dramatic reaction imposed on the environment by the plants such as was exhibited in the annual deposition of pine litter in North Carolina (Billings 1938). A mild replacement of the calcium content of the soil is annually effected by deposition of leaves of red cedar and flowering dogwood. Such local enrichment is neither excessive nor important in providing a better site for oak germination, since the pH of the surface soil does not alter much during the succession as a whole.

Bonner (1950) and Keever (1950) have demonstrated the effects of toxicity of decaying parts of various species such as Encelia and Leptilon. It would appear that living plants may also exude substances inimicable to other species, but this phe-

nomenon requires further substantiation. As yet, succession in New Jersey cannot be explained in terms of pure reaction.

STABILIZATION

Stabilization of the climax community requires its self-perpetuation through adequate maintenance of reproduction. Mettler's Woods, the nearest approach to climax, may exhibit shortcomings in this respect: the number of oak seedlings is very low. While hickory seedlings are more common than oak, they are far surpassed in numbers by dogwood seedlings. Similarly, there are more saplings of dogwood than oak. Oak sprouts are, of course, observed, as are a few seedlings on the margin of the forest (cf. Oosting & Kramer 1946), but the prolonged maintenance of this woodlot as an oak-hickory forest is questioned because of its unique position in the general area.

There are few large or small forests in Somerset County and these are often maintained as game preserves. Mettler's Woods represents such an area in a wide radius of ever-increasing suburbanization. The population-pressures of squirrels, chipmunks, and other small animals feeding on acorns and hickory nuts are probably intensified by the restrictions on hunting. As long as huge populations of rodents and crows and other birds, annually deprived of more feeding ground, converge on Mettler's Wood's, the number of nuts escaping destruction will be small. When the low supply of food will begin to make inroads on the animal population and the ratio between the demand and food is gradually diminished, then an improvement in the status of Mettler's Woods may be expected. But disregarding the problem presented by the animal population for the moment, a less pessimistic view of the forest may be obtained if one stops to realize the reproductive requirements of an oak forest. While the number of seedlings per 100 sq m seems very low, it may represent an amount sufficient to replenish the forest. Many of the larger oak trees are over two hundred years old, and it is not improbable that they may survive another century. Replacement of these slowly expiring monarchs requires but a few seedlings. Admittedly, the larger the number of seedlings, the more assured is the forest of its future dominants, but for the occasional tree toppling during a wind-storm or dying from some other cause, there is an adequate number of sprouts, saplings, or seedlings any one of which may take its place. It is for this reason that the consideration of Mettler's Woods as representing a climax community may be warranted.

SUMMARY

The successional pattern on upland sites on the Triassic shales of the Piedmont Plateau in New Jersey has been studied, and the following are its salient features:

1. *Vegetation*

a) Fields abandoned for one year contain the subsequent herbaceous dominants in insignificant

amounts, but the immediate dominants are usually *Ambrosia artemisiifolia* and *Oenothera parviflora*.

b) By the second year of abandonment, *Solidago nemoralis* assumes dominance and remains important for approximately fifteen years, when *S. juncea* supercedes it and becomes the dominant herb of 60-year-old fields.

c) *Aster ericoides* increases to dominancy by the fifth year and may maintain high coverage for approximately twenty more years.

d) *Andropogon scoparius* (with some *A. virginicus*) assumes dominancy by the fifteenth year and remains important for more than forty-five years.

e) *Juniperus virginiana* invades young fields within the first few years and becomes the dominant arborescent species for over sixty years.

f) Most of the arborescent species of the oak-hickory forest enter the succession before the red cedar is mature. Oaks and hickories are well established and are in the understory by the sixtieth year of abandonment.

g) The two dominant shrubs of the succession are *Rubus flagellaris* and *Rhus radicans*, the former demonstrating maximum coverage in fields abandoned for approximately twenty-five years, the latter at approximately sixty years, the oldest abandoned field studied.

h) As succession progresses, the number of annuals and non-indigenous species decreases and the number of those species whose fruits are disseminated epizoically or endozoically is increased.

2. *Soils*

There appears to be a lack of decisive correlation between any of the investigated physical and chemical properties of the soil and the age of abandonment of the fields. Discrepancies appeared to be due to the slight but important textural differences between the soils. It may be demonstrated that the organic matter content, moisture-holding capacity, total exchange capacity, conductivity, and nitrate content may increase slightly towards the oak-hickory forest, but this cannot be demonstrated in fields of varying textural qualities. This situation could only be ascertained if a single field were investigated periodically over a protracted period of time.

3. *Roots*

Depth of penetration of the roots increases with the age of abandonment. The greatest density of roots is noted in the upper 15 cm. of the soil in every stage. The smallest roots are encountered in the upper horizons, the larger ones in the lower horizons. There is no evidence in the comparative root systems of the earlier and later arborescent dominants to indicate their differential competitive ability.

4. *Causation*

Causation of succession is to be sought in a study of the life-cycles and tolerances of the various species including those members of the animal population instrumental in seed dispersal. An elucidation of the reactions of all the species—both plants and animals—to variations in light and its effect may aid in deciphering the successional pattern whether in connection with interspecific competition, survival of seedlings of diverse species, or the activities of certain rodents while introducing the dominant arborescent species of the climax forest into younger fields.

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THE UPLAND CONIFER-HARDWOOD FORESTS
OF NORTHERN WISCONSIN

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INTRODUCTION

A long-term study of the plant communities of Wisconsin, involving the examination of large numbers of stands of each major vegetation type, was begun in 1945. To date, prairie relics (Curtis & Green 1949), pine relics (McIntosh 1950), and upland hardwood forests (Curtis & McIntosh 1951) have been investigated. The present paper deals with a study of 116 stands of upland conifer-hardwood forests in northeastern Wisconsin, with emphasis on the relations of the various stands to each other and to their physical environment. Many persons contributed invaluable aid during the progress of the work. Dr. Grant Cottam directed much of the field work in 1950 and contributed stimulating advice throughout the study. Drs. Robert McIntosh, Max Partch, and Forest Stearns, Miss Margaret Gilbert, and Messrs. Orlin Anderson, William Randall, and Edward Terrell all helped in the collection of field data. Drs. F. D. Hole, F. T. Thwaites, and R. F. Bryson gave advice on problems of soils, geology, and meteorology respectively. To all these and to all others who helped in other ways, we extend our sincere appreciation.

LITERATURE REVIEW

The conifer-hardwood forests of the northeastern half of Wisconsin lie within the region of the Lake Forest Formation of Weaver & Clements (1938).

According to these authors, "the Lake Forest consists of a single association, in which *Pinus strobus*, *P. resinosa* and *Tsuga canadensis* are the climax dominants." Associated with these climax trees are *Pinus banksiana* and *Thuja occidentalis* in subclimax roles. No mention is made of any deciduous associates, except for *Betula papyrifera* and *Populus tremuloides* which are thought to be fire trees derived from the Boreal Forest Formation. The herbs are said to be "common to boreal forest or deciduous forest for the most part," with few or no characteristic species. This description is based largely on the observations of Sargent (1884). Bergman & Stallard (1916) reported that the northeastern part of Minnesota was occupied originally by a climax association of *Pinus strobus* and *P. resinosa*. They trace the development of this association through a detailed series of distinct associes, including the *Larix laricina-Picea mariana* and *Abies balsamea-Betula papyrifera-Betula lutea* forests in the hydrosere and the *Juniperus virginiana* and *Pinus banksiana-Betula papyrifera* forests in the xerosere. The final climax forest was thought to be a mixture of *Pinus strobus* and *P. resinosa* or pure stands of either, although "it seems probable the *P. strobus* would finally replace *P. resinosa*."

Weaver and Clements, Bergman and Stallard and other proponents of the Pinus or Pinus-Tsuga climax forest all relied on early word-descriptions of the region. No supporting quantitative data as to actual stand composition are given by these authors and there is no evidence that such data were ever actually compiled.

A series of more recent studies on the forests of the region, based upon detailed phytosociological investigations, have failed to establish the terminal nature of Pinus or Pinus-Tsuga forests. Thus Gleason (1924), Kittredge (1934), Eggler (1938), Graham (1941), Potzger (1946) and Stearns (1951), to cite but a few, all have demonstrated that the Pinus forests eventually are replaced by a deciduous forest in which *Acer saccharum* is a universal dominant, accompanied by such trees as *Fagus grandifolia*, *Betula lutea*, *Tilia americana* or *Tsuga canadensis* in different portions of the region. The trend of upland successions appears to be quite uniform throughout the area, with *Pinus banksiana* and *Quercus ellipsoidalis* as the pioneer species, followed by *Pinus resinosa*, *Pinus strobus* and *Quercus rubra* and eventually by *Tsuga canadensis*, *Betula lutea* and *Acer saccharum* and other shade tolerant deciduous species on the most mesic sites. The actual composition of the terminal forest is exceedingly variable and subject to great local deviations. In her recent discussion of this forest (as the Hemlock-White Pine-Northern Hardwoods region) E. Lucy Braun (1951) indicated that in eastern Upper Michigan there may be at least four types of terminal forest, depending upon minute variations in the underlying morainal topography—*Fagus-Acer saccharum*; *Acer saccharum-Fagus*; *Acer saccharum-Fagus-Tilia*; and *Acer saccharum-Tilia-Ulmus americana-Fagus*.

Many of these recent investigators have indicated by their comments or their tables of data that they considered the forest to be composed of discrete communities, which could be described in terms of their leading dominants. Some have made separate communities when the same dominants were present in different order, as Fagus-Acer vs. Acer-Fagus. Very few of the studies (and none in Wisconsin) have included a sufficient number of stands so that effective judgment could be made as to the actual areal extent of these discrete communities nor as to the degree of variation present among the minor members of the assemblage. In the upland deciduous forests of the prairie-forest border region of southwestern Wisconsin (Curtis & McIntosh 1951) it was found that no two stands of the 95 examined had the same arrangement of their first four leading dominants. No discrete communities could be recognized—"rather the entire series of communities formed a continuum in which a definite gradient was exhibited from initial stages composed of pioneer species to terminal stages composed of climax species." One of the aims of the present study was to determine whether discrete communities could be found in the northeastern portion of the state, or whether a vegetational continuum existed there also.

DESCRIPTION OF THE REGION
Location

The area included in this study is bounded on the west by the Minnesota-Wisconsin boundary, on the north by Lake Superior and the Michigan-Wisconsin border, and on the east by Lake Michigan (Fig. 1).

Fig. 1. Map of Wisconsin, showing location of stands studied. It is 270 miles between the easternmost and the westernmost stands.

The southern boundary is a tension zone, a region which extends across Wisconsin in a general northwest-southeast direction, and which is delimited by a marked vegetational change and by the range limits of many northern and southern plants. Curtis & McIntosh (1951) and Lindsay (1951) give extended discussions of this boundary.

Climate

Borchert (1950) has reviewed the evidence for the overall climatic control of major vegetation regions and has shown the close correlations between vegetation boundaries and the mean pathways of air mass movements. He places northeastern Wisconsin in his type I, which is characterized by snowy winters and reliable summer rains. The snow cover is usually deep enough to protect the soil from frost penetration to any great depth and often prevents any freezing of the soil. Low summer temperatures combine with frequent rains to reduce evaporation to a low level.

Geology

With the exception of a small portion in the Driftless Area, all of the study area in northern Wisconsin has been glaciated. The bed rock beneath the glacial drift over a large part of the area is pre-Cambrian igneous and metamorphic rock. In the eastern part of the state it is Niagara dolomite, Silurian in age. West of the escarpment of this very resistant rock are Ordovician shales, sandstones, and dolomites, and beneath these strata are the Cambrian sandstones which extend into the Driftless Area and form the bedrock there.

Although there were several glaciations, the difference between them is not as important a factor

in the growth of vegetation as is the variation in topography, soil, and drainage caused by any one of them. The drift of the Cary substage of the Wisconsin glaciation occupies approximately one half of the study area. Smaller areas of the Valders, Mankato and Iowan substages of the Wisconsin also occur.

VEGETATIONAL HISTORY

The last great advance of the ice sheet took place some 11,000 to 12,000 years ago according to radiocarbon analyses of the timber in the forest bed at Two Creeks, Wisconsin (Arnold & Libby 1951). This forest was pushed over during the advance of the ice, and was left covered by about 15 to 20 feet of drift which kept it from decomposing rapidly. At some unknown later date, the final recession of the ice left the land open to colonization by plants. The first trees to invade the land were Abies and Picea, according to the many pollen analyses made in the region (Wilson 1937; Potzger 1943). These were followed by *Pinus* sp. and finally by Tsuga and Betula.

There have been periods of drought during which fires were prevalent. According to Indian legend, there was a great fire about 1550. The largest trees of *Pinus strobus* in the region began their growth about 1600; they could have started on the land left open by the fires (Graham 1941).

Recorded quantitative data on the forests of Wisconsin date back to the original governmental land survey which was made between 1830 and 1866. At the time of the survey, large areas in the southern part of the study area in central Wisconsin were covered with savanna-like stands of *Pinus banksiana*. Before 1850 this land was ravaged by fires, both those set by natural causes and those set by Indians to drive game and to improve berry crops. Shortly after that date, the land was settled by white men who did much to stop the fires, thus allowing young trees to grow into the dense forests found in the region today.

The northern part of the study area was originally covered with an almost continuous stand of dense forest; nearly all of this land has since been logged to a greater or lesser degree. That land which was close to the rivers was the first to be lumbered because water was the only means of transportation of the logs to the sawmills. At a later date, narrow gauge railroads were built back into the upland areas away from the streams. The locomotives on these railroads started many fires in the slash: these fires often burned unchecked for many days through both virgin forest and logged-over land. Lumbering operations on a large scale continued from about 1860 to 1920. By that time nearly all of the merchantable timber had been either cut or burned. Since 1920, with adequate protection from large-scale fires. the forests have been recovering from the effects of the logging era. It is obvious from this discussion that tracts of untouched virgin forest are exceedingly rare today.

METHODS

FIELD METHODS

Inasmuch as this study was undertaken to investigate the phytosociological composition of all types of upland northern forests, with particular attention to the range of variability from stand to stand, it was necessary to use rapid, accurate methods of taking data. It has been found that the random pairs method (Cottam & Curtis 1949) gives the greatest amount of usable data for the smallest investment of time and labor. It was, therefore, used in these surveys with a slight modification. Instead of recording the saplings along a belt transect between each pair of trees, as in the original method, the four closest saplings to the point were recorded. This was done to give a larger and more representative sample of the reproduction. All of the data taken were recorded on printed forms designed to simplify both the recording of the field data and the compilation of these data in the laboratory.

The criteria used in the selection of stands for study were the same as those of Curtis & McIntosh (1951), namely, that the stands be natural forests at least 15 acres in size, on upland land forms not subject to inundation, and free from recent disturbance such as fire, grazing, or cutting. Some second growth stands which started shortly after early logging were included if no disturbance had taken place during the lifetime of the stand. The stands were located by correspondence with foresters, county agents, soil conservation service men and others who might have knowledge of the existence and whereabouts of suitable areas.

Soil samples were obtained in nearly all stands by digging three small soil pits and collecting and pooling samples from the appropriate horizons. However, because of lack of funds or time for analysis of all the layers, only the A_1 layer was collected in many of the stands. In work done by Partch (1949) and by McIntosh (1950) it was shown that correlations between this horizon and the vegetation are more marked than with any other horizon, since this horizon is most quickly affected by the decomposition of plant remains. The soil samples were prepared for analysis by grinding in a Wiley mill until the particles passed through a 2 mm screen. Analyses for calcium and potassium were done by the State Soils Laboratory. The pH of each sample was moisture-holding-capacities were determined by the determined with a glass electrode potentiometer. The inson (1949).

The most rapid method of field operation for a two-man team was for one man to carry the small quadrat stakes and to do the pacing between trees. The other man carried the data board and recorded the presence of herbs in the quadrats while the first measured the basal area of the trees and the distances between them. An ice pick was used to hold one end of the tape while the distance was being measured. The tapes were graduated in feet on one side and in basal area on the other so that they could

be used for either measurement. A tree was arbitrarily taken as any woody stem over 4 inches d.b.h. (12 square inches basal area) and a sapling as any woody stem between 1 and 4 inches d.b.h.

The taxonomic nomenclature used is that of Gray's Manual of Botany, 8th edition. Any plants which could not be identified in the field were collected, marked, and identified later, if possible. Specimens of most of the plants so identified may be found in the University of Wisconsin Herbarium.

LABORATORY METHODS

The simplest method of transferring the field data to summary data sheets in the laboratory was to record the diameter-size (dominance) of trees of each species separately. From this list of sizes, the number of trees was also found. The number of points of occurrence was obtained by counting on the field data sheets. Relative density and dominance were found by simple mathematical calculation. The relative frequency (Curtis & McIntosh 1950) was found by totalling the points of occurrence and dividing the points of occurrence of each species by this total. These three relative values were summed to give a single number, the *importance value* (I.V.), which shows the relative ecological importance of each species in the stand better than any one of its component measures. The importance values for all species in each stand add to a constant total of 300; the values for a given species may thus be compared between stands upon an equal basis. The relative density of the saplings and the frequency for each of the herb and shrub species were also obtained for each stand.

Although an effort was made to choose homogeneous stands in the field when collecting the data, it was felt that an objective homogeneity test should be given to each stand. The Chi Square Test (Snedecor 1946) was applied, using the four field data sheets with four sequential sets of 10 random pairs each as sample groupings of trees in a stand. Since this test requires at least five individuals per theoretical sample, only those tree species represented by at least 20 individuals could be used. It was assumed that if the major species were homogeneous, any deviations from homogeneity in the minor species were unlikely or insignificant. Since there were over 100 stands represented, it was felt that use of the one percent level of confidence in the test was justified. On this basis, two stands were discarded, leaving 116 stands. The probability of homogeneous distribution exceeded 20 percent in most of these stands.

RESULTS

FOREST COMPOSITION

As a first step in the interpretation of the data, the total number of tree species encountered was determined. Thirty-one large woody species (27 trees and 4 which sometimes reach tree size) were found in the 116 stands. Of these, 15 species were the most prominent in at least one stand as indicated by the importance value. In the 116 stands, 56 different

arrangements of the first and second species, 85 different arrangements of the first three, and 105 different arrangements of the first four were found.

Of the 56 different arrangements of the first two species, only 5 pairs occurred in more than 4 stands. The most frequent pair, which occurred in 9 stands, was *Pinus strobus* first, *P. resinosa* second. There were 36 pairs which were found only once. If certain species were interdependent, one might logically expect that they would be found together frequently in nature. It would appear from the above observations that this is not the case.

The next step was to explore the possible relations of the tree species to their environment. To do this, it was necessary to reduce the data to a more understandable form. As a start toward this end, Table 1 was prepared using the method of leading dominants

TABLE 1. Average importance value of trees in stands with given species as leading dominant—104 stands.

No. of Stands	Leading Dominant	Acer saccharum	Tsuga canadensis	Betula lutea	Acer rubrum	Quercus rubra	Betula papyrifera	Pinus strobus	Pinus resinosa	Populus tremuloides	Quercus ellipsoidalis	Pinus banksiana
23	Acer saccharum	145	25	21	7	22	6	1	..	1	..	..
23	Tsuga canadensis	40	152	47	11	3	5	4	3	..	..	..
6	Quercus rubra	27	1	3	29	138	23	10	8	5	3	..
6	Betula papyrifera	48	8	7	27	16	108	19	1	29	1	..
19	Pinus strobus	12	6	2	24	12	12	150	39	9	5	..
9	Pinus resinosa	3	..	1	12	15	14	56	156	24	4	2
4	Populus tremuloides	11	..	..	10	29	34	14	19	140	..	..
4	Quercus ellipsoidalis	..	..	..	5	7	1	11	9	9	103	56
10	Pinus banksiana	..	..	..	3	3	3	13	12	14	36	213

(Curtis & McIntosh 1951). In the column at the left are the numbers of stands in which the species shown in the second column were the leading dominants. In the head of the table are these same species plus *Acer rubrum* and *Betula lutea* which never achieved prominence in any stand but which were common in many. The figures in the body of the table indicate the average importance value of the species across the top in the stands dominated by the species at the left. For example, in the 23 stands dominated by *Acer saccharum*, the average importance value of *Tsuga canadensis* was 25, or in the 6 stands dominated by *Quercus rubra*, the average importance value of *Betula papyrifera* was 23. With this method of leading dominants, it was possible to arrange the species in a reasonable phytosociological order by assuming that *Pinus banksiana* was the most pioneer species and *Acer saccharum* the most climax and by placing the other species some place between these two extremes by a trial and error method, such that all columns of numbers, both horizontal and vertical, most nearly approached smooth curves. On the basis of the order shown in Table 1, a climax adaptation number (Curtis & McIntosh 1951) was assigned to each tree, with values arbitrarily ranging from one

for *Pinus banksiana* to ten for *Acer saccharum*. Tree species which occurred together frequently and hence might be presumed to have nearly similar environmental requirements received nearly similar adaptation numbers, while species of widely divergent requirements received widely spaced numbers. The climax adaptation numbers of the minor tree species not shown in Table 1 were assigned on the basis of their close association with one or more of the major species in the table. The final list of climax adaptation numbers for all species encountered in the study is given in Table 2.

TABLE 2. Climax adaptation numbers of tree species found in stands studied.

Tree Species	Climax Adaptation Number
Pinus banksiana	1
Quercus ellipsoidalis	2
Quercus macrocarpa	2
*Populus balsamifera	2
Populus tremuloides	2
Populus grandidentata	2
Pinus resinosa	3
Pinus pensylvanica	3
Quercus alba	4
Prunus serotina	4
Prunus virginiana	4
Pinus strobus	5
Betula papyrifera	5
*Juglans cinerea	5
Acer rubrum	6
*Acer spicatum	6
*Fraxinus nigra	6
*Picea glauca	6
Quercus rubra	6
Abies balsamea	7
*Thuja occidentalis	7
*Carpinus caroliniana	7
Tsuga canadensis	8
Betula lutea	8
*Carya cordiformis	8
Fraxinus americana	8
Tilia americana	8
Ulmus americana	8
Ostrya virginiana	9
Fagus grandifolia	10
Acer saccharum	10

*Climax adaptation number of these species is tentative only, because of their low presence in the stands studied.

These climax adaptation numbers may be looked upon as an estimated measure of the ability of the species to compete successfully in the total environmental complex of an *Acer saccharum* forest. The higher the number, the more successful is the species, while the lower the number the less successful. Thus, in Table 1, it can be seen that *Pinus banksiana* never

occurred in any stands dominated by *Acer saccharum* while *Tsuga canadensis* and *Betula lutea* attained relatively high average importance values in those stands. On the other hand, *Acer saccharum* never occurred in any stands dominated by the two most pioneer species—*Pinus banksiana* or *Quercus ellipsoidalis*. It perhaps should be emphasized at this point that these adaptation numbers are not absolute measures of physiological characteristics of the species but only relative indices of the behavior of the species in this region. Thus *Pinus strobus* with a number 5 is more climax than *Pinus resinosa* with a number 3, but the actual value 5 is dependent in part upon the presence in the same region of the extreme pioneer species *Pinus banksiana* which has arbitrarily received the value of one. If the latter species were not present, the actual number assigned to *Pinus strobus* might be different, *but* it would have the same relative relation to *Pinus resinosa* as before.

The climax adaptation number was multiplied by the importance value of each species in each stand. The sum of these products gave a weighted figure which was called the *continuum index* (C. I.) of the stand. It is obvious that this final index can vary between 300 and 3000 because the total of the importance value is always 300 and the component segments of the total are multiplied by figures from 1 to 10. The continuum index is a measure of the total environment as expressed by the total tree composition. Its main use is in ranking the stands along a gradient, such that those stands which are most similar from the standpoint of their trees are placed close together, while those with greater dissimilarity are more remote from each other. Presumably, a similar order of stands could be arrived at by other means than the use of climax adaptation numbers and measured importance values. The significant feature is the result, not the method of operation. If the order of stands is phytosociologically correct, then the behavior of the individual species in those stands should follow reasonable patterns. If the order is wrong, then individual species would exhibit only chance variations and random fluctuations.

To check this behavior of individuals, various methods of arranging and averaging the data were tried. In Table 3, a portion of the original data for the 17 most important species is shown, for stands which have been arranged in the continuum index order. The selection was made by taking the data from every other stand from the complete set. The four highest importance values for each species are shown in bold face type. Upon detailed inspection, it can be seen that these optimum figures are preceded and followed by an increasing or decreasing series of values, although the trends are not perfectly smooth, being interrupted by low values or missing values. This irregularity is more easily visualized when the importance values for each species are plotted against the continuum index for the stands, as has been done in Figure 2, for *Abies bal-*

Table 3. Original data for importance values of 17 species and for three soil characters.

| Stand Number	Continuum Index	*Pinus banksiana*	*Quercus ellipsoidalis*	*Populus tremuloides*	*Populus grandidentata*	*Pinus resinosa*	*Quercus alba*	*Pinus strobus*	*Betula papyrifera*	*Acer rubrum*	*Quercus rubra*	*Abies balsamea*	*Betula lutea*	*Tsuga canadensis*	*Ulmus americana*	*Tilia americana*	*Ostrya virginiana*	*Acer saccharum*	Calcium in A1 layer (100's lbs. per acre)	pH of A1 layer	WRC of A1 layer
084	356	272	4	9		12				4									4.3	5.1	77
066	375	237	46	7	6		5												4.3	4.9	36
068	467	164	117	4			16												2.9	4.6	54
098	560	157	95	14				5	15	14									2.1	4.6	164
055	594	178		30	7	46		39											1.4	4.5	102
049	664	122	100				62	6		11									2.9	4.0	118
082	721	181				34		59	4	4		4							1.1	4.6	99
067	749	100	62	4	8	7	101				5								2.9	4.7	54
113	848	10		68		204		14	3	14									6.4	4.3	148
064	868			194	24	7		34	16	14	4								–	–	–
039	934		132		27		107		4	3	22								2.1	4.7	60
115	954				4	268		16	12										7.2	5.4	110
150	984		6	54	162	5			30		35	3							–	–	–
053	991			63		159		74	4										–	4.3	400
140	1082			62		116		121											3.6	5.1	281
044	1107		8	4	20	153	11	82	3		18								–	–	–
141	1168	7	4	31	33	65		145			3	7		3					3.6	5.2	400
132	1209				5	138		157											0.7	4.5	269
059	1290		5	4		96		186	7			3							–	–	–
070	1363		32	16			109	46			84								4.3	5.7	43
050	1403		3		3	41		243	10										7.1	4.9	69
089	1436					41		238	5	10	4								0.7	5.2	124
107	1508			15		38		180	3	15		40				3		3	6.4	5.2	106
106	1518			12	18	51		42	21	54	84	3					3	12	8.6	5.5	180
090	1573			12		15	11	166	39	13	3	3		16			3		3.2	5.5	65
105	1582			17		9		158	3	9	82				3	6		6	8.6	5.0	225
043	1640				5		39	121	7	65	22				20	3	3	3	5.4	4.9	89
147	1750				7	22		4	52	20	143		10	7		3	3	19	5.4	5.2	272
153	1807				10	10	3	56	96	6	47	16				3	3	57	2.1	5.3	288
086	1888					61		54	12	4			11	158					0.4	4.0	192
102	1950		4				10	13	20	26	141	3				19	7	35	2.7	4.9	91
095	1966				4			106		58			19	84		17	6	21	1.1	5.3	67
101	2060			12			11		3	9	124		7	49	3	17	6	89	12.5	5.5	80
119	2173		17						3			29	7		3	17		73	35.7	6.1	373
139	2215							11		41		6	12	176	4			11	3.2	4.6	270
138	2234							12		11		3	81	111				15	2.1	3.7	409
104	2287			10				8		19	59		15		17	20	12	102	16.0	4.5	289
116	2314		7		28				29	24	33	8					11	161	7.2	5.2	209
111	2366								11	32	5		52	157		4	3	33	8.6	5.0	223
063	2379									13		6	60	206				15	–	–	–
136	2404							12				25	72	145			3	33	5.4	4.6	400
085	2430							15	12				15	198			9	24	14.3	5.5	258
062	2464												66	182		16		31	7.1	5.6	210
134	2502								28			7	84	87		8		82	4.3	4.4	335
118	2520											7	29	160		19	11	66	12.9	5.0	497
125	2553												58	106	25	34	4	73	3.6	5.4	398
034	2591						10	35		5	8	3	8	27		13	23	115	45.7	5.6	365
121	2617										4		35	69		49	8	111	28.6	5.4	131
103	2636												8		80	30	6	124	42.8	5.5	305
135	2711											4	22	86	3	19	18	149	42.9	6.9	119
080	2747												40	34	11	22	21	162	6.4	4.8	158
094	2780												17	13	8	44	13	183	23.6	5.3	129
076	2817												3	3	23	8	30	184	51.0	7.6	137
133	2852												12		32	16	10	220	10.7	5.7	526
114	2938										3		6			8	7	268	10.0	5.0	157
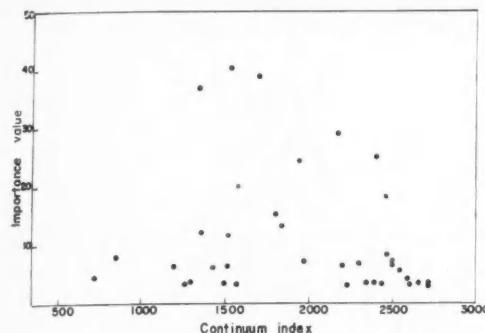
FIG. 2. Importance values of *Abies balsamea* for stands arranged in order of continuum index. Each point represents a separate stand.

samea. The scatter diagrams for all species were like this one, in that they took the shapes of a solid Gaussian curve, or a part of one. This was true even for the minor species, which do not have much influence on the magnitude of the continuum index.

Because of various chance situations, it is obvious that even where optimum environmental factors are present, a particular species may be absent in a given stand, while in another stand with approximately the same environment, it may be the dominant tree. However, it can never be dominant in any stand with an environment far removed from its optimum. Hence, the solid normal curves.

To reduce the information still further, the stand tables were segregated into groups of 300-unit continuum index size classes and the importance values of each species in each group averaged. Constancy percentages (number of stands of occurrence of each species within the sample of 80 trees expressed as a percentage of the total number of stands in each

TABLE 4. Average importance value of trees by 300 unit continuum index classes. Only those species with an average value over 5.0 in at least one class are included.

Species	300	600	900	1200	1500	1800	2100	2400	2700
Pinus banksiana	192.1	72.9	2.2	1.2					
Quercus ellipsoidalis	65.3	58.0	21.6	11.6	1.6	0.5	0.5		
Quercus macrocarpa	6.0	36.1	0.4		0.2				
Populus tremuloides	20.4	33.3	29.5	25.5	12.6	5.5	2.1	0.8	
Populus grandidentata	5.2	4.3	29.5	19.5	8.4	4.0	4.3	0.8	
Pinus resinosa	11.0	33.8	95.8	85.8	20.8	9.4			
Quercus alba	3.2	18.8	29.8	19.0	9.0	2.6	1.6		
Prunus serotina		4.6	0.5	6.9	1.1	0.9			
Pinus strobus	8.1	25.7	54.9	94.6	80.5	38.8	1.6	1.0	0.5
Betula papyrifera	3.4	2.5	7.3	20.8	36.0	47.0	10.5	4.2	
Acer rubrum	1.6	4.4	8.2	28.9	34.4	20.3	24.1	5.5	0.4
Quercus rubra	2.6	2.1	17.5	38.4	36.3	42.1	24.5	9.4	1.1
Abies balsamea		1.3		4.0	8.8	7.6	4.1	3.8	0.7
Thuja occidentalis				0.6	0.3	1.1	20.8	1.3	
Tsuga canadensis				0.4	2.6	31.0	39.4	37.7	28.2
Betula lutea				0.4	2.0	9.6	31.7	49.9	19.5
Tilia americana			0.6	0.8	1.1	5.7	7.4	19.0	14.6
Ulmus americana		0.7		0.8	1.6	1.2	2.3	9.4	22.4
Ostrya virginiana				0.2	0.7	2.0	4.0	6.9	12.1
Fagus grandifolia						3.4		7.7	37.2
Acer saccharum			0.8	5.2	17.1	26.7	58.0	83.7	160.5

group) were also determined. The summations of importance values for the main species are shown in Table 4. The differences between species with regard to amplitude of their environmental tolerances and peakedness of their modes is well displayed by these values.

It seemed possible to show the optimum conditions for each species in a more precise manner than that conveyed by these 300-unit averages. In order to accomplish this, the average importance value of each species was calculated for each 100-unit segment of the continuum index. For example, *Acer saccharum* occurred in 11 stands which had continuum indices ranging between 2500 and 2600. Its average importance value in these 11 stands was 93. The number of stands in which a tree occurred was used in this case rather than the total number of stands in a given range as in the 300-unit averages.

Minor irregularities in the curves result from peculiarities of groupings due to the choice of end points for the 100 unit segments. For example, the average importance value of *A. saccharum* for the 100-segment from 2490 to 2590 was 92 and for the segment 2510 to 2610, 95, both of which were slightly different from the value of 93 for the segment from 2500 to 2600. The simplest method for avoiding these irregularities is the use of a moving average. This was accomplished by the formula:

$$B = \frac{n_1 a + 2n_2 b + n_3 c}{n_1 + 2n_2 + n_3}$$

where B is the smoothed value of average b, and n_1, n_2, and n_3 are the numbers of stands included in averages a, b, and c, respectively. These smoothed points were then plotted on a graph and a free hand curve was drawn through them. Figure 3 is a graphical representation of the entire smoothing process for the *Pinus strobus* curve.

In Figure 4 are the smoothed curves for the five
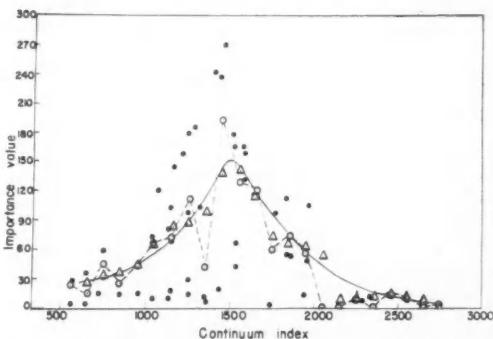
FIG. 3. Graph illustrating method of smoothing data for *Pinus strobus.* The solid circles are the actual importance values for each stand in which this species appeared. The open circles (connected by dotted line) are the same values averaged by 100-unit continuum index classes. The triangles are the values obtained by the use of the smoothing formula discussed in the text. The smooth line is a free-hand line through the triangles.

most important trees: *Pinus banksiana, P. resinosa, P. strobus, Tsuga canadensis,* and *Acer saccharum.* Figure 5 shows the curves for the trees of intermediate importance, and Figure 6 shows the curves for those of lesser importance. Note the differ-
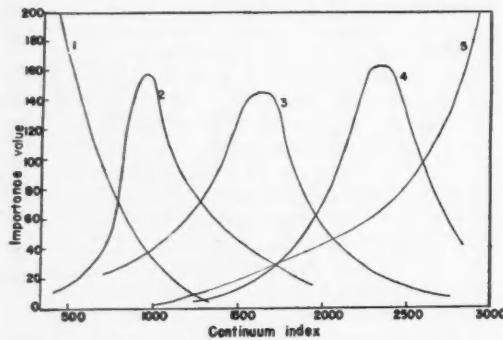

FIG. 4. Importance value curves for the five leading species. The curves were obtained by the method illustrated in Figure 3. 1 is *Pinus banksiana,* 2 is *P. resinosa,* 3 is *P. strobus,* 4 is *Tsuga canadensis,* and 5 is *Acer saccharum.*
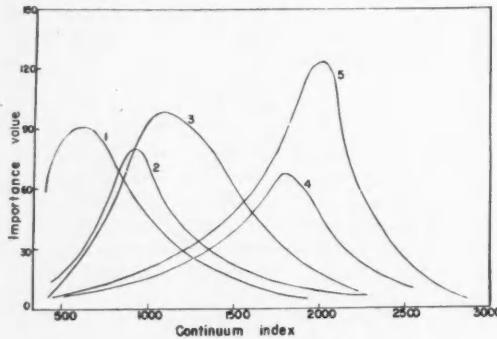

FIG. 5. Importance value curves for five intermediate species. 1 is *Quercus ellipsoidalis,* 2 is *Populus tremuloides,* 3 is *Quercus alba,* 4 is *Betula papyrifera,* and 5 is *Quercus rubra.*
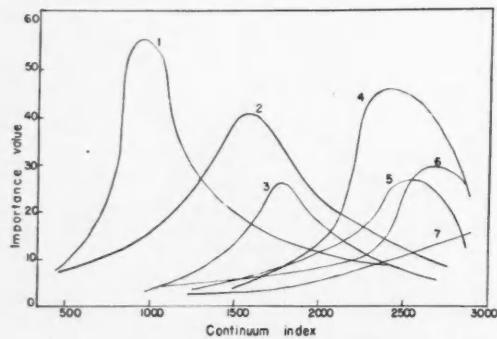
FIG. 6. Importance value curves for seven lesser species. 1 is *Populus grandidentata,* 2 is *Acer rubrum,* 3 is *Abies balsamea,* 4 is *Betula lutea,* 5 is *Tilia americana,* 6 is *Ulmus americana,* and 7 is *Ostrya virginiana.*

ent scales on the ordinates of these three graphs. The purpose of all these curves is not so much to show the maximum importance of any particular tree under optimum conditions, as to present graphically a composite picture of the relationships of different trees to each other, as indicated by the relative position of their modes along the continuum index.

The relative density of saplings as compared to the importance value of mature trees of the same species is shown for *Populus tremuloides* and *Betula lutea* respectively in Figures 7 and 8. The stands of optimum growth for the two age classes are seen to approach each other more closely as the climax nature of the species increases. The other species show relationships similar to those given here as examples.

The preceding use of average importance values, based on a combination of relative number and relative size of the trees, tends to obscure some important aspects of the behavior of individual species. The average basal area of the trees, for example, increases with increasing continuum index. Thus,
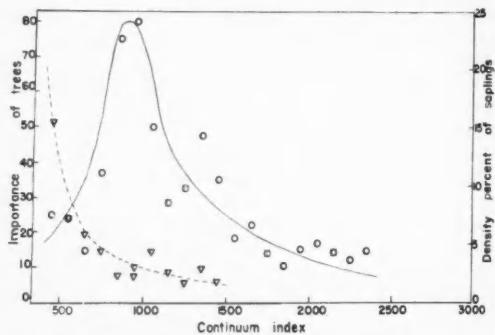
FIG. 7. Comparison of saplings and mature trees of *Populus tremuloides.* The open circles are average importance values of trees 4″ d.b.h. or over by 100-unit continuum index classes. The triangles are average density percentages of saplings (1″ - 4″ d.b.h.), also by 100-unit classes.
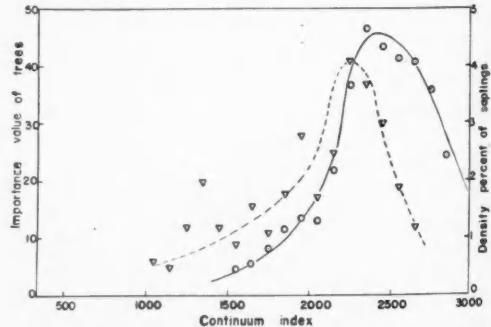
FIG. 8. Comparison of saplings and mature trees of *Betula lutea.* The open circles are average importance values of mature trees, and the triangles are average density percentages, both by 100-unit continuum index classes.

Pinus strobus in stands from 300 to 600 CI has an average basal area per tree of only 34 square inches. This increases steadily with increasing index to a peak value of 495 square inches in the most climax stands from 2700 to 3000 CI. The maximum importance value of the species per stand is reached in the range from 1200 to 1500 CI, while the percentage of stands containing this species is high (constancy over 70%) in the broad range from 600 to 2100 CI. On the other hand, the number of saplings reaches a maximum in the range from 600 to 900 CI. Thus we see that *Pinus strobus* enters the forest early, with large numbers of saplings. These mature and reach maximum importance about midway in the continuum, although they are of medium size at this point. Thereafter, their numbers and total importance decreases, although they continue to be represented in a great majority of the stands. Reproduction ceases about two-thirds of the way along the continuum and the species disappears from many of the stands. In those stands still retaining the species it reaches great size, with maximum trunk area achieved in the most climax stands, although the species has almost reached the vanishing point in terms of number of individuals on these sites. This information is summarized in a set of graphs in Figure 9, while similar information is given for *Pinus banksiana*, *Pinus resinosa*, *Tsuga canadensis* and *Acer saccharum* in Figs. 10 to 13, respectively.
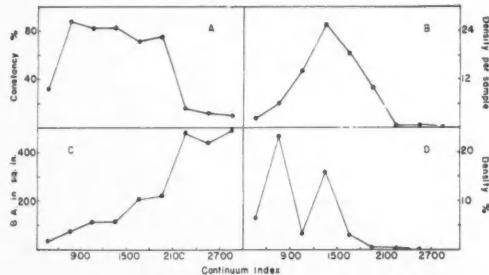
FIG. 9. The behavior of *Pinus strobus*. Graph A is the constancy (percent of stands in which the species appeared in the 80-tree sample). B is the actual number of mature trees per 80-tree sample, C is the average basal area per tree in square inches, while D is the relative density of saplings. All values are averages by 300-unit continuum index classes.
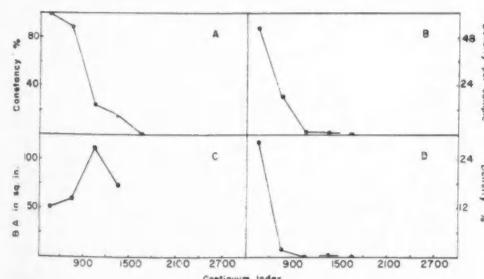
FIG. 10. The behavior of *Pinus banksiana*. Graphs A, B, C, D are on the same bases as in Figure 9.
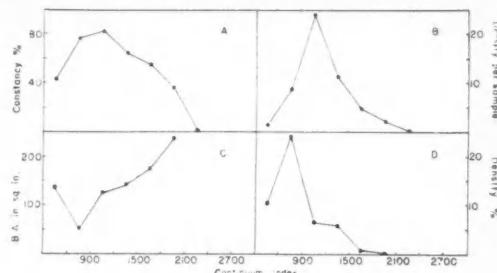
FIG. 11. The behavior of *Pinus resinosa*. The graphs are similar to those in Figure 9.
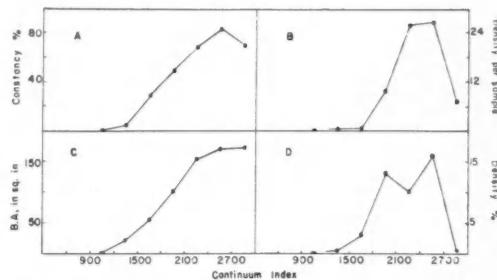
FIG. 12. The behavior of *Tsuga canadensis*. See Figure 9.
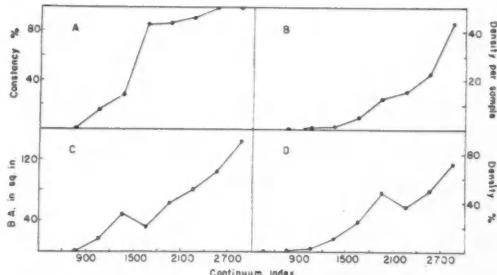
FIG. 13. The behavior of *Acer saccharum*. See Figure 9.

By means of these sets of graphs the main dynamic forces functioning in the continuum can be seen at a glance.

Not only do the trees and saplings show preferences in habitats, but the herbs also exhibit very marked environmental selectivity. Figure 14 shows the position along the continuum index in which *Aquilegia canadensis*, *Arisaema atrorubens*, *Comandra richardsiana*, *Lycopodium lucidulum*, and *Moneses uniflora* flourish. These were chosen as plants each typical of a different habitat. On the basis of preliminary calculations nearly all of the other herbs show a similar marked selectivity for some particular kind of habitat as measured by the trees.

SOILS

It has been well established that vegetational succession is a soil building process (Braun-Blanquet 1932; Lutz & Chandler 1946) and that certain soil
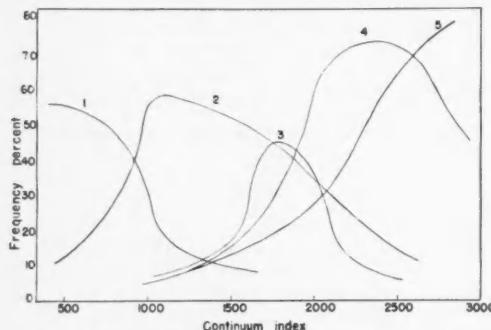
FIG. 14. Average frequencies of five typical herbs in stands arranged in continuum index order. The lines were smoothed by the process illustrated in Figure 3. 1 is *Comandra richardsiana*, 2 is *Aquilegia canadensis*, 3 is *Moneses uniflora*, 4 is *Lycopodium lucidulum*, and 5 is *Arisaema atrorubens*.
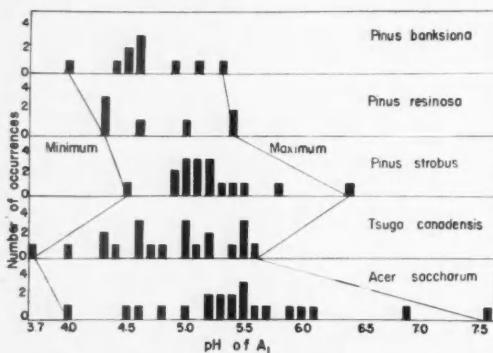

FIG. 15. Frequency distributions of pH values of the A_1 soil horizons in stands with the indicated species as leading dominants.

factors are greatly influenced by the plant cover. In a glaciated region like northern Wisconsin, with a wide variety of soil parent materials and topographic drainage conditions, a perfect correlation between soil properties and vegetation can scarcely be expected to occur. However, in spite of the variability, definite trends can be observed. Figure 15 shows the relation of the pH of the A_1 layer to the most important tree species. Because of the difficulties encountered in interpreting average pH values, it was felt that a bar graph would provide a better understanding of the variability of this factor and would, at the same time, demonstrate the influence of the vegetative cover. It is evident that the maximum, the minimum, and the modal lines all show very similar trends; all increase through *Pinus strobus*, drop off sharply in Tsuga stands, and rise sharply again in *A. saccharum* stands. Tsuga litter evidently forms very acid decomposition products.

Figure 16 shows the relation of the specific gravity of the dry A_1 to the continuum index. A greater proportion of incorporated organic matter causes it to fall off as the climax is approached.

Figure 17 shows the relationship of the continuum index to the moisture holding capacity and to the total amount of water which the A_1 is capable of holding at field capacity. The marked trend is probably partly due to the greater amount of incorporated organic matter in stands with a high continuum index and partly due to the higher silt and clay content of these soils. The greater depth of the A_1 layer in the stands with a high continuum index increases the total amount of water which may be held. These results are in close agreement with the findings of Partch (1949).

The total amount of available calcium in the A_1, as shown in Figure 18, is much greater in high continuum index stands than in any other type of forest. This is partly due to the much greater depth of the A_1 layer of soil. It has also been suggested that the more climax types of vegetation tend to concentrate certain mineral nutrients in the upper soil layers. This is thought to be accomplished by the removal of these nutrients from the subsoil, their concentration in the leaves, where they remain when the leaves are shed, and the decay of the resulting litter without the production of decomposition products which are capable of leaching out the nutrients.

As is shown in Figure 19, there is almost no trend
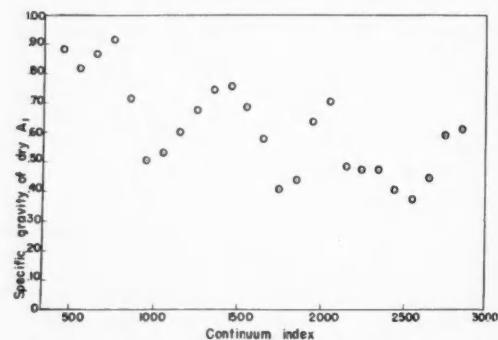
FIG. 16. Specific gravity of screened samples of the A_1 soil horizons of stands arranged in continuum index order. Points are average values by 100-unit classes.
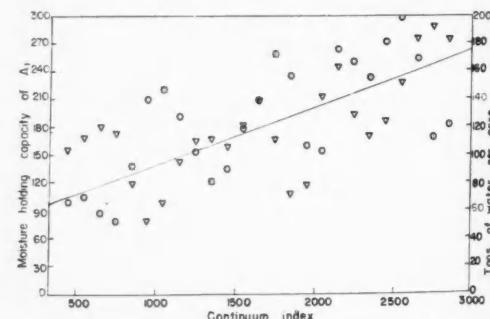

FIG. 17. Moisture holding capacity of A_1 horizon in percent and total water held in the entire A_1 horizon at field capacity in tons per acre. Points are average values by 100-unit classes.
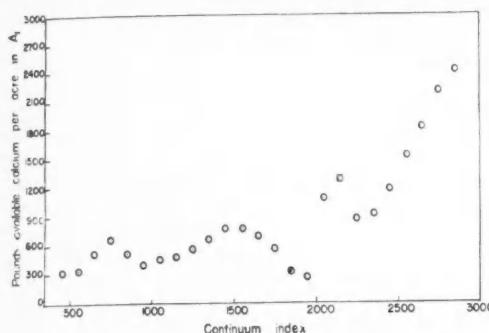
FIG. 18. Available calcium in the A_1 horizon in pounds per acre. Points are average values by 100-unit classes.
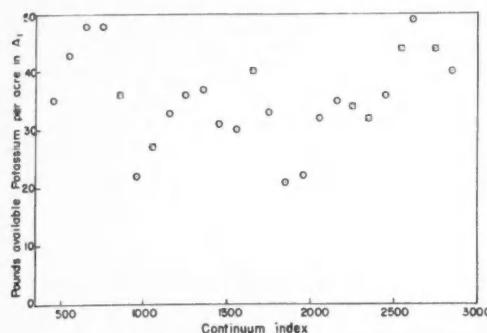

FIG. 19. Available potassium in the A_1 horizon in pounds per acre. Points are average values by 100-unit classes.

in the amount of available potassium when plotted against the continuum index. It is not to be expected that every soil factor will give a good correlation with the continuum index. In the soils of the sampled stands, it appears that there is enough potassium for good growth of trees, and none of the trees seem to have the ability to concentrate it as they do calcium. Further research is needed to provide a complete answer to the problem.

This is not a complete picture of the soils relations. Other factors such as organic matter, available phosphorus, specific conductivity, silt-clay percentage, or settling volume could be investigated. It is likely that some of these would be, and others would not correlate with the continuum index. Mogens Koie (1951) has given figures on soil and vegetation characters for 102 stands of Danish oak woods that show great similarities with the results presented here and in addition emphasize the importance of the mechanical composition of the subsoil. It is probable that subsoil studies in the Wisconsin conifer-hardwood forests would be of considerable interest.

SUMMARY OF STAND COMPOSITION ALONG THE CONTINUUM

The following generalized descriptions of stands along different ranges of the vegetational continuum

index may be of value in summarizing the great mass of numerical data upon which the preceding results were based.

STANDS WITH LOW CONTINUUM INDICES

The trees most prominent in stands with indices below 800 are *Pinus banksiana*, *Quercus ellipsoidalis*, and *Populus* spp. *Pinus banksiana* is a fire tree, an intolerant species of extreme pioneer nature. In Wisconsin it usually grows on sandy soils which are the scene of frequent fires because they dry out so rapidly. In other parts of its range, it may occur on heavier soils. In order to persist for more than one generation, *P. banksiana* must have fire; otherwise more tolerant species replace it. Although the individual trees are killed by fire, the species is perpetuated because many of the cones do not open until the heat of a fire dries them out sufficiently. The seeds thus liberated can germinate on the mineral soil, and the young trees can grow unhindered by any canopy, often producing even-aged stands over large areas. When white men first came to central Wisconsin, they found the land covered by *P. banksiana-Quercus ellipsoidalis* openings with prairie herbs and brush between the trees. The usual spacing between trees was about 100 feet, but they were sometimes ¼ mile apart (Brown 1950). The average density was from 2 to 8 trees per acre. Following the recent control of the fires, the trees have filled in the openings, but as yet, little type change has taken place. Densities now are 160 to 250 per acre. *Pinus resinosa*, *P. strobus*, *Quercus alba*, *Q. rubra*, and *Acer rubrum* are slowly invading the *P. banksiana* forests and will eventually replace them.

Quercus ellipsoidalis is another intolerant species often found occurring with *Pinus banksiana* in dry sandy places. It is perpetuated by fires which kill off more mesic trees, but do not kill the Quercus. The above-ground portions of the tree may be destroyed, but the roots are not, and they remain in the ground as grubs which send up new shoots after each fire. The exact taxonomic nature of this tree is very puzzling. Many variations in morphological characters may be found, with obvious intergrades to *Q. rubra* and *Q. velutina* and possibly *Q. coccinea* as well. These putative hybrids or introgressives are usually found on heavier soils, while the populations on sandy soil seem to be relatively pure *Q. ellipsoidalis*.

The *Populus* species usually are found in places which have been burned over. They are relatively intolerant of shade. For these trees to become established, exposed mineral soil must be available at the time the seeds are shed since these seeds are viable for only a few days. Both *Populus tremuloides* and *P. grandidentata* often grow on fairly good soil and there they are quickly replaced by more climax tree species. In central Wisconsin on the sand plains nearly all of the Populus trees may be found growing on sites which are underlain by clay. *Populus balsamifera* was found only rarely in this study.

There is but little reproduction of the dominant species in these low index stands; instead, such trees

as *Pinus resinosa, P. strobus, Betula papyrifera, Abies balsamea,* and *Acer rubrum* comprise most of the saplings. The canopy is quite open, and consequently a great deal of brush and many low-hanging branches are present and often make these stands rather forbidding places in which to work. The litter of the forest floor is usually dried out rapidly by the sun and is not of very great thickness. The herbaceous species common in these stands include such plants as *Arctostaphylos uvaursi, Comandra richardsiana, Comptonia peregrina* var. *asplenifolia,* and *Vaccinium angustifolium.* The soils under these stands have a poorly defined leached (A_2) layer. The depth of the unincorporated organic matter (A_0) ranges between $\frac{1}{2}$ and $1\frac{1}{2}$ inches, as does the depth of the incorporated humus layer (A_1). The pH of the latter usually ranges between 4.5 and 5.5. The soil types on these sites are Plainfield, Vilas, and Omega sands.

STANDS WITH MEDIUM LOW CONTINUUM INDICES

In most of the stands which have continuum indices between about 800 and 1700 the dominant trees are *Pinus resinosa* and *P. strobus. Acer rubrum* is often quite prominent, but seldom attains dominance. Some old trees of *P. banksiana, Quercus ellipsoidalis* and *Populus* sp. may also be present. On other sites, *Betula papyrifera* may be quite important.. Although it is not a shade tolerant tree, *Pinus resinosa* does invade *P. banksiana* stands and is also able to survive in *Populus tremuloides* stands and to replace these short-lived trees when they die. It sometimes seeds in on burned-over areas which have no large trees. The bark on this tree, once it has reached maturity, is quite fire-resistant. Consequently, it is not uncommon to find a forest which has very large trees of *P. resinosa,* some with fire scars, surrounded by small second growth usually consisting of *P. banksiana, Quercus ellipsoidalis, Populus tremuloides,* and some *Pinus resinosa.* It grows most often in association with *P. strobus* with which it often forms majestic forests.

Although in the opinion of Stallard (1929), Weaver & Clements (1938) and others, both *Pinus resinosa* and *P. strobus* are climax species, neither is self-perpetuating on uplands in Wisconsin. The impression that these were the climax species probably stems from reports by the early explorers who travelled by boat. They saw many of the shores lined with these two species, and could see their tops towering above the rest of the forest on the uplands, and assumed that these were the climax trees along with Tsuga. Although *P. strobus* is more shade tolerant than *P. resinosa,* it also is unable to survive beneath its own canopy. It is frequently found replacing *Populus* sp., and sometimes found replacing *P. banksiana* or *Q. ellipsoidalis.* It is also capable of invading burned-over areas or old fields directly. The trees on old fields are often damaged in various ways and are therefore likely to be misshapen. Kittredge (1934) and Stearns (1950) both discuss successional relationships and age of the forests containing *P. strobus.*

Acer rubrum has, perhaps, the broadest amplitude of environmental tolerance of any tree found in northern Wisconsin. It can be found in almost any type of stand, but is usually not of much importance. It is a rather short-lived tree, and rarely grows larger than 18 inches in diameter. Although quite tolerant of shade, it may also become established very quickly in any opening. It regenerates readily after a fire, both from stump sprouts and from seeds.

Betula papyrifera seems to be more shade tolerant than either of the *Populus* species or *Quercus ellipsoidalis.* Like Populus, it is a short-lived tree, and must have disturbances in order to be perpetuated.

In these medium low index stands, the reproduction consists mainly of those trees which reach their optimum development in stands with higher indices. These include *Acer saccharum, Tsuga canadensis, Betula lutea* and *Abies balsamea.* Very few saplings of Pinus, a few of *Betula papyrifera,* some of *Quercus rubra,* and more of *Acer rubrum* are also found. The canopy is dense enough so that the trees are self-pruned and little brush grows beneath them. On the forest floor is a thick mat of litter in various stages of decomposition, with such plants as *Chimaphila umbellata, Epigaea repens, Aquilegia canadensis, Linnaea borealis, Polygala paucifolia,* and several species of *Pyrola.* In comparison with the soils of *P. banksiana* stands, the A_0 layer here is thicker (1 to 3 inches), the A_1 is thinner ($\frac{1}{4}$ to 1 inch), and the A_2 is $\frac{1}{2}$ to 3 inches and quite well defined. The pH of the A_1 is higher, ranging between 5 and 6. The soil types on these sites are Onamia and Omega loams or sandy loams. There are also a few Vilas and Milaca sandy loams.

STANDS WITH INTERMEDIATE CONTINUUM INDICES

Between continuum indices of about 1500 and 2000 are found stands which often have a great many species, some hangers-on such as large trees of *Pinus resinosa,* many young trees of a more shade-tolerant nature, as well as a few intermediate species. The most important trees in this range are *Quercus rubra, Pinus strobus, Betula papyrifera, Acer rubrum,* and *Abies balsamea.*

Quercus rubra is a tree of medium tolerance, and is probably perpetuated by fires. It is much longer-lived than either Populus or *Betula papyrifera,* and for this reason as well as its greater shade tolerance, is often found in very mesic stands as large trees.

Abies balsamea, although fairly shade tolerant, does not thrive in the dense shade cast by more mesic stands of *Acer saccharum,* which usually replace it. Heart rot caused by *Polyporus anceps* injures the trees to such a degree that they seldom survive long enough to reach a diameter in excess of 10 inches. Because of their inability to grow beneath an *Acer saccharum* canopy, and because of their short life, these trees need frequent disturbances to be perpetuated.

The reproduction of these intermediate index stands consists mainly of very shade tolerant species such as *Acer saccharum, Tsuga canadensis, Betula*

lutea, and *Ostrya*. These forests, like the Pinus forests, have a fairly dense canopy and are relatively free from brush. The litter decays more rapidly and consequently is not as deep as in the pine stands. Herbs common in these stands include *Corallorrhiza maculata*, *Moneses uniflora*, *Thalictrum dioicum*, and *Viola adunca*. The same soil types found in the *Pinus resinosa-Pinus strobus* forests occur in this range, with the addition of a few Auburndale and Kennan silt loams.

STANDS WITH MEDIUM HIGH CONTINUUM INDICES

Over a range of continuum indices between about 1900 and 2600, *Tsuga canadensis* is usually the dominant tree. *Betula lutea*, *Acer saccharum*, *Fagus grandifolia* (in eastern Wisconsin), *Tilia americana*, and *Thuja occidentalis* are often quite abundant. An occasional giant tree of *Pinus strobus* may stand out above the rest of the forest.

Tsuga is a tree which presents troubling problems that have provoked a great deal of research. Briefly stated these are: how does a stand of *Tsuga* originate and is it self-perpetuating? According to Hough (1936) and Hough & Forbes (1943) *Tsuga* probably seeds in best after a disaster. They found that in a large forest in northwestern Pennsylvania the *Tsuga* trees could be separated into definite age classes. If *Tsuga* were capable of becoming established under a mature forest canopy, the trees would be of all ages. Stearns (1951) made age determinations on many trees in Wisconsin and found that some had been suppressed for many years before finally gaining a place in the canopy, but that others started in the open. He found a suggestion of periodicity such as that described by Hough. Lutz (1930) and Graham (1941) both felt that *Tsuga* was capable of self-perpetuation but Lutz did mention that in dense stands, reproduction was scanty.

Of the 116 stands included in this study, *Tsuga* was replacing the overstory in only three, one a *Quercus rubra* forest, one a *Pinus strobus* forest and the third a *P. resinosa-P. strobus* forest. The stand of *O. rubra* had been logged and burned approximately 50 to 60 years ago. The two Pinus stands were both even-aged, slightly more than 100 years old. It is likely that the *Tsuga* needs some organic matter on which to germinate (rotten stumps and logs are preferred) and at least a partial canopy to protect the young trees from direct sunlight. In general it grows best on mesic sites of fairly uniform moisture content. The organic matter and protection from direct sun aid in moisture conservation. If these environmental conditions plus a plentiful supply of seeds are present, then *Tsuga* may become established.

Once established, a stand of *Tsuga* is long-lived. However, it has been observed by many authors that *Tsuga* does not reproduce well in its own shade. Stearns (1951) found that in the stands he studied, there were two times as many Acer trees as Tsuga trees and one hundred times as many Acer saplings. Gleason (1924) studied the forests in Cheboygan County, Michigan, and says, "records . . . extending

TABLE 5. Comparison of total densities of *Acer saccharum* and *Tsuga canadensis* by basal area classes.

Tree Species	TOTAL NUMBERS OF TREES BY BASAL AREA CLASSES			
	Saplings	Trees		
	1 to 11 sq. in.	12 to 80 sq. in.	81 to 320 sq. in.	Over 320 sq. in.
Acer saccharum...	935	156	102	16
Tsuga canadensis.	573	296	538	107

over a period of thirteen years . . . indicate that reproduction of hemlock is very rare, and the general deficiency of hemlock saplings shows that this condition has prevailed for many years. Almost all the hemlock trees . . . are veterans. After their death . . . hemlock will practically disappear as a component of the (maple-beech) association."

In the present study, those stands in which Tsuga was unquestionably the leading dominant were segregated for special study. Table 5 shows a comparison of Tsuga with *Acer saccharum*, the second dominant in these stands. This table indicates quite clearly that even in stands where Tsuga is now supreme, it will lose out in the future. The great majority of the large trees are Tsuga, but this preponderance greatly diminishes in the smaller size classes and is reversed in the saplings. A noticeable characteristic of these Tsuga forests is the relative scarcity of saplings of any kind, as well as the fact that most of the few Tsuga saplings present are very stunted or have dead tops and probably will never become trees. The deficiency of Tsuga saplings in current-day stands has also been attributed partially to deer browsing (Swift 1946). This, no doubt, has been an important factor in local areas in the last two decades with a rapidly increasing deer population. From all this, it appears that in a stand in this area which remains undisturbed, Tsuga will gradually lose out to the hardwoods, particularly *Acer saccharum*.

It would be very interesting to know whether a natural catastrophe in a Tsuga forest would allow regeneration. Wind storms powerful enough to blow down large areas of these shallowly-rooted trees need occur only once every century or two if regeneration does take place. Information on this subject may soon be available, for during the past two years, several wind storms of hurricane force have blown down nearly all the trees in several areas of the Flambeau River State Forest in Sawyer County, Wisconsin. The trees on these areas were predominantly Tsuga, and if no salvage operations are carried out, very valuable information on the ability of this species to reseed after a disaster will be provided.

Betula lutea is very often found growing with Tsuga. It is a tree which is fairly shade tolerant, and germinates best on decaying organic matter, particularly old rotting logs, as does Tsuga. It is a very long-lived tree, and grows to tremendous size.

Although it almost never is the dominant tree in a stand, it often is one of the most conspicuous species, because of its distinctive, shaggy bark.

The majority of the saplings present in these stands are *Acer saccharum* with a small amount of Tsuga and a few of the other shade tolerant species mentioned. Where Fagus is present, it often dominates the reproduction. A few saplings of *Acer rubrum* and Abies are also usually present. The canopy in these forests is usually very dense and the light on the forest floor very dim. Common herbs include *Clintonia borealis, Coptis groenlandica, Dryopteris disjuncta, Dryopteris phegopteris, Equisetum sylvaticum, Lycopodium annotinum, Lycopodium lucidulum, Mitella nuda*, and *Oxalis montana*.

On sites where Tsuga is the dominant tree, the A_0 layer is usually quite thin because of the rapid decomposition of the needles. It ranges from almost none up to one inch. The A_1 is also very thin and about the same depth as the A_0. The A_2 is much thicker, ranging from $1\frac{1}{2}$ up to about 5 inches. It is very well defined and is usually ashy gray in color. In the B horizon of deeply podzolized soils a cemented layer can often be found. The pH of the A_1 in these stands is low, seldom exceeding 5.0. Soil types founds in these stands are Milaca, Iron River, Kennan, and Stambaugh sandy loams or loams.

STANDS WITH HIGH CONTINUUM INDICES

Stands which have a continuum index over 2500 are usually dominated by *Acer saccharum*. Associated with this species are *Ulmus americana, Tilia americana, Betula lutea, Tsuga canadensis, Ostrya virginiana*, and *Fraxinus americana*. The reproduction consists mainly of *Acer saccharum*, but a few saplings of all the others are present. Almost everyone who has studied the forests of this region agrees that *Acer saccharum* is a climax tree species. As has just been shown, it can replace the very tolerant Tsuga. It may be found in many types of forest, but is very rare in *Pinus banksiana* and *Quercus ellipsoidalis* stands. Although it is the most shade tolerant species which ranges throughout the entire area studied, a pure stand is seldom approached because disturbances of various kinds provide enough openings in the canopy for other slightly less tolerant trees such as *Ostrya virginiana, Tilia americana, Betula lutea, Tsuga canadensis* and *Ulmus americana* to become established (Stearns 1951). In the extreme eastern part of the state, it occurs in climax forests with *Fagus grandifolia*, a tree which is equally capable of self-perpetuation.

Tilia americana is another shade tolerant tree which is often quite prominent in these stands, but which is almost never the dominant tree. It does not reproduce well beneath a complete canopy of *Acer saccharum*, but if some of the latter trees are removed, it often reproduces profusely in these openings. This tree, like *Acer rubrum*, sends up many root suckers and consequently is able to persist almost indefinitely from a single successful seedling establishment.

Ulmus americana is very similar to *Betula lutea* and Tilia in its habitat requirements, and is often found growing with these species in stands dominated by *Acer saccharum* and Tsuga. It is a fast growing, long-lived tree, often the largest in a stand. The taxonomic position of this tree is not well defined; most of the trees in northern Wisconsin possess characteristics of both *U. americana* and *U. rubra* although no pure strains of *U. rubra* are present.

Ostrya virginiana is a small, slow-growing, very shade tolerant tree which is often found as a minor component of the understory in the most mesic stands. It never is a dominant species, and almost never is a member of the overstory of trees.

The canopy of these climax stands is so dense that the lack of light by midsummer causes the forest floor to be almost devoid of green herbaceous plants. Herbs characteristic of this habitat are *Adiantum pedatum, Allium tricoccum, Caulophyllum thallictroides, Hydrophyllum virginianum, Laportea canadensis, Mitella diphylla. Sanguinaria canadensis* and *Uvularia grandiflora*, all of which are also present in stands above 2500 in the upland forests of southwestern Wisconsin (Curtis & McIntosh 1951).

The litter decomposes very rapidly, leaving the forest floor nearly bare by the end of summer in some places. The A_1 ranges from 1 to 4 inches in depth and has a crumb structure in contrast to that in lower index types where it is usually not developed well enough to have any clearly defined structure. The A_2 is often poorly delimited and is sometimes practically non-existent, but reaches a maximum of 4 inches depth in some sites. The wide range of associated species may account for this variation in the A_2. The pH of the A_1 may be as high as 7.5 and is seldom below 5.5. Since *A. saccharum* succeeds the other trees, many soil types are found. These include Vilas, Omega, Onaway, Antigo, Santiago, Kewaunee, Kennan, Miami, Auburndale, and Hibbing. Other types may also be present.

DISCUSSION

INFLUENCE OF STUDY METHOD ON RESULTS

There have been two main types of methods used in the study of plant communities in the past. These may be called the "trained-eye" methods and the quantitative measurement methods. In the first, the investigator has presumably trained himself, by long experience in the region, to recognize various plant communities on sight and to be able to distinguish critically between what are significant species changes and what are but trivial variations in species composition. He also must be able to judge accurately the abundance of each species present, regardless of the stratum of its occurrence. In practice, this method involves the subjective choice of a stand or series of stands which fit the investigator's concept of a particular community, followed by an observational study which results in a statement of the dominants or important plants of the community, estimations of their abundance or cover, and perhaps indications as to some of the characteristic but less important species. If a series of stands of several

related communities has been studied, there may be statements concerning the fidelity of the species in addition. In capable hands, this method has produced results of highly significant value to our understanding of the vegetation of many regions of the world. However, it appears to have two very serious drawbacks—one is the scarcity of investigators with the wide field experience necessary and the second is the lack of any means whereby the accuracy of the results may be checked. This last goes beyond mere error of observation, but refers also to the impossibility of using the results of this method to validate the fundamental community concepts upon which it is based. In other words, the trained-eye method does not permit other ecologists to ascertain for themselves whether the stand studied was really one community, several communities, or only a part of one community, nor does it provide any information whereby the underlying concept of the actual existence of discrete communities in nature may be tested.

The quantitative measurements methods are varied as to procedure but all have in common the direct determination of some measure of vegetation. usually number, size, or distribution of the component species of the community. Providing the measurement technique is adequate, these methods give reproducible results which may be checked by other investigators and which offer some possibilities of independent estimation of community variation. They are not wholly free from subjective error, however, since the choice of stands to be studied is one of the most important factors affecting the results (Ashby 1948). If the investigator studies only those stands which fit a preconceived notion of community limits, the quantitative methods offer no firmer basis than trained-eye methods for the critical appraisal of the real existence of distinct communities.

It is perhaps impossible to avoid completely all subjective judgments in ecological field work. In the present study, the use of objective criteria for the selection of stands to be investigated minimized the errors usually present in such choice, but subjective judgment was needed in assessing degree of disturbance and type of land form. These judgments of physical conditions were necessarily subject to error, but it is believed that such errors are open to correction and do not unduly prejudice the results. In any case, we believe that the study of many stands, chosen in as objective a manner as possible, and examined by statistically acceptable quantitative methods. provides results which may be critically examined by other workers and which offer internal evidence bearing on the validity of the conclusions offered.

SUMMATION OF CURRENT RESULTS

In the present case. the quantitative measurement of number. size and distribution of the tree members of 116 stands of upland forest in northeastern Wisconsin failed to indicate the existence of discrete communities that could be considered as separate, identifiable entities by any objective criteria. Rather, the results indicated that all stands studied were parts of one great community complex, arranged along a gradient from pioneer conditions of low moisture, high light, low soil organic matter, and low soil base content to climax conditions of medium moisture, low light, high soil organic matter and high base content. Each species achieved optimum growth along a narrow range of this gradient, with definite limitations to its well-being on either side of this optimum range. No two of the major species reach optimum conditions in the same range and none of the species appeared to form groups having the same range. As a result, no communities could be recognized on the basis of their tree composition, while preliminary consideration of the herbs likewise offered no basis for the objective recognition of separate entities. The stands formed a vegetational continuum, with a continuously varying series of species, sorting themselves along an environmental gradient whose main controlling features result from the interactions of the plants themselves.

According to Ganong (1907) "any plant stands where it does for the reason that the physical demands made by the structure and habit it happens to possess overlap in some degree the physical conditions prevailing in that place, and the better they match the more nearly does the plant find its optimum, and the worse they match the more slender is the hold of the plant upon that place." In the flora of any region, there is an assortment of species, some of which have "physical demands" matched by pioneer environments, some by climax environments, and some by various degrees in-between. Some of the species have a broad environmental tolerance and others are narrowly limited in their physical requirements. In a region (such as northeastern Wisconsin) where differences in topographic relief are slight, and where soil parent materials, although varied, are not sharply separated from one another, maximum opportunity is presented for slight differences in physiological behavior to express themselves in different species groupings. The results of this study indicate that there is a continuous series of species which match all segments of the full range of environment of the region, with no large groups bunched in the same environment and no environments devoid of adapted species.

SIMILAR RESULTS OF OTHERS

An essentially identical situation was found for the upland hardwood forests of southwestern Wisconsin (Curtis & McIntosh 1951). There, a vegetational continuum ranging from *Quercus macrocarpa* at the pioneer end to *Acer saccharum* at the climax end covered approximately the range in environments as does the present series. It is of interest that the two continua are very similar in their terminal forests, both containing *Acer saccharum, Tilia americana*, and *Ostrya virginiana* and a uniform group of characteristic herbs. while the initial and intermediate forests are dominated by species of *Quercus* in the southern region and by species of *Pinus* in the north.

Whittaker (1951, 1952) studied the vegetation of the Great Smoky Mountains by means of a series of transects, arranged along observable moisture or altitudinal gradients. He sampled all stands which were not clearly successional at regular intervals along these gradients. When the measures of importance of each tree species (in this case, relative densities) were plotted against the observed gradient, a series of normal or binomial curves were obtained, with no two of the major species showing modes in the same portion of the gradient (compare his Fig. 1 with our Fig. 3, 4, & 5). The most mesic large tree species were *Aesculus octandra*, *Tilia heterophylla*, *Acer saccharum*, *Betula lutea*, and *Tsuga canadensis*, while the most xeric species were *Pinus virginiana*, *Pinus rigida*, *Quercus marilandica* and *Quercus coccinea*. Intermediate positions were assumed by *Acer rubrum*, *Quercus montana*, and *Quercus alba*. If the climax adaptation value of 10 is assigned to *Tilia heterophylla* and a value of 1 to *Pinus virginiana* and intermediate values to the others on the basis of the relative spacing of their modes between these two, the values given in Table 6 are obtained. The same table shows the values found in this study and in the southwestern Wisconsin study (Curtis & McIntosh 1951) for the species in common. The minor differences between the ratings are perhaps not so significant as the rather remarkable degree of similarity. Whittaker (1951) concludes that the "species were not organized into association units" and the "Climax vegetation here is a complex continuum of plant populations."

The occurrence of a continuously varying natural

TABLE 6. Comparison of climax adaptation numbers in three regions.

Species	Whittaker Great Smokies	Curtis & McIntosh Southwest Wisconsin	Brown & Curtis Northeast Wisconsin
Pinus strobus........	3.3	...	5.0
Quercus velutina......	3.9	2.0	...
Quercus alba.........	4.1	4.0	4.0
Acer rubrum.........	6.4	7.0	6.0
Quercus rubra........	6.8	6.0	6.0
Fagus grandifolia....	7.8	...	10.0
Tsuga canadensis.....	8.6	...	8.0
Betula lutea.........	9.3	...	8.0
Acer saccharum......	9.4	10.0	10.0

phenomenon correlated with a habitat gradient is not confined to forest sociology. The catena concept of the pedologists (Bushnell 1942) appears to be nearly analagous to the continuum idea. Thus, in a soil catena, certain soil profile characteristics change gradually and continuously with position along a topographic slope. In the Miami catena, there may be Clyde soils at the bottom of the slope and Bellefontaine at the top, with Miami, Crosby and Celina in between. In their midranges, these soil types are clearly distinct, but they gradually merge in their boundary regions. A knowledge of their systemic

relations to each other and to the environment is essential to a complete understanding of their origin and their use.

The idea of a vegetational continuum as opposed to a series of discrete plant associations, associes or communities is not new. Gleason (1929), in his admirable discussion of the individualistic nature of plant communities, proposed as an example the flood plain forests of the Mississippi River. There a continuous transect study along the length of the river would reveal the gradual elimination of some species and the addition of others such that the forest at Lake Itasca in Minnesota is manifestly a completely different assemblage from that at Lake Pontchartrain in Louisiana, yet no one can draw a line and say that north of it is one forest and south of it another. Different ecologists, if they made such a transect study, would in all probability draw more than one line and each would draw them in different places. This would result from the vain attempt to compartmentalize a continuous variable into discrete segments. Such an Aristotelian approach in science, the search for absolutes, for ultimate truths, for discrete classification of facts, has gradually been giving way in recent years to the belief that "the laws of nature are . . . simply in our ways of conceptualizing data, and the absolute is . . . our need for security" (Cameron 1948). In the related field of taxonomy, Womble (1951) in developing a method of differential systematics to overcome the difficulties inherent in the classification of continuous variables, points out the limitations of categorical reason and states that "dynamic processes must be sought, not in the differentiated, but in the differentiating." The continuum concept is a means whereby the system of continuous variates may be readily visualized and where the search for underlying dynamic processes may proceed unhampered by the limitations of any artificial, pigeonhole-classification system.

This trend away from the old schematic aligment of a series of circumscribed units in an all-encompassing hierarchy, like the "packaged and shelved organization of a gigantic food mart" (Egler 1951) has been gaining support in Europe as well as in America, although there are still many adherents to the concept of a pulverized vegetation of small entities with discrete boundaries. As Gisin (1951) says, "L'idee d'une unite elementaire sembler hanter beaucoup d'esprits." There have been many attempts to solve the problems of community delimitation (Begrenzung) in terms of internal evidence rather than on the basis of preconceived community entities, in an effort to avoid the "circulus vitiosus" (Katz 1933) inherent in the use of characteristic species as indicators of associations. These attempts have usually led to some system of correlation analysis (Tuomikoski 1942) or interspecies association (Agrell 1945) which emphasizes that species have independent tolerance ranges related along gradients in a manner very similar to the continuum concept presented here.

The nature of a continuum and its use in com-

munity description may be clarified by analogy with the visible light spectrum. The different wavelengths of this portion of electromagnetic radiation have different properties with respect to penetration through glass, one result of which is their separation upon passage through a prism. The resulting rainbow spread of colors is a familiar sight. None but the color blind can fail to distinguish the red end from the blue end and most observers can easily locate the primary colors, at least in their midregions. The boundaries between blue and green, or red and orange, or other pairs, however, are not so readily distinguished. The degree of separation of these colors is largely under the control of the investigator and his instruments. Colored glass filters of appropriate construction will absorb most of the wavelengths and allow only a small band to pass. Such separation is imperfect, however, and truly pure colors can be had only with a monochromator. The physicist does not attempt to class his wavelengths by color name—rather he specifies the exact range in Angstrom units.

In the forest continuum, all but the vegetation-blind will be able to distinguish the opposite ends of the spectrum—the *Pinus banksiana* forests below an index of 500 from the *Acer saccharum* forests above an index of 2800. For many, if not most, purposes, the intermediate forest types can be named conveniently according to their leading dominants as *Pinus strobus* forests or *Tsuga canadensis* forests, analogous to the use of red glass filters or green glass filters. But precise investigations call for the more exact delimitation of the continuum range under study. Just as all red glass does not transmit the same wavelengths, so all *Pinus strobus* forests are not alike. Recognition of the fact that there is a gradient in forest composition correlated with an observable cline in habitat factors permits the designation of a particular stand or series of stands with any degree of precision requisite to the study. Regardless of whether we call it a spectrum, a catena or a continuum or whether we term its study "gradient analysis" with Whittaker, "correlation research" with Tuomikoski, or "differential systematics" with Womble, the concept of continuously varying, closely correlated sets of natural phenomena seems to offer great promise in furthering our understanding of vegetation.

SUMMARY

1. The upland conifer-hardwood forests of Wisconsin were studied in a random sample of 116 stands distributed through 24 countries in the northeastern half of the state. Information on tree species, numbers and sizes was obtained by use of the random pairs method, while shrubs and herbs were studied by the quadrat method. Soil samples for acidity, nutrient and moisture analysis were collected in each stand. The relative importance of each tree species in each stand was expressed as an importance value, resulting from a summation of relative density, relative frequency, and relative dominance figures.

2. When the stands were grouped according to their leading dominants, there were 15 groups if based on the single leading species, 56 groups if based on the first two species in order, 85 groups based on the first three and 105 groups based on the first four species. Calculation of average importance value for all species (by groups arranged according to the leading dominant) resulted in an order of species from *Pinus banksiana* at the xeric end to *Acer saccharum* at the mesic end of the series. Climax adaptation numbers were assigned to all species, based upon the locations of their stands of optimum growth relative to Pinus and Acer stands. The adaptation numbers were used to weight the importance values of each species in each stand and thus to arrive at a single index value for each stand. These indices for the 116 stands covered the range from 356 to 2938 (out of a possible range of 300 to 3000).

3. The results indicated that all of the stands studied were part of one great community complex, arranged along an environmental gradient from xeric pioneer conditions to mesic climax conditions. No discrete communities could be recognized on the basis of their tree composition along the gradient. Rather, the entire group formed a continuum, with a continuously varying series or species which matched all segments of the full range of environments of the region, with no large group bunched in the same environment and no environments devoid of adapted species. Many soil factors, including acidity, calcium content, and water holding capacity were positively correlated with the vegetational continuum.

4. Descriptions of forests in five broad segments of the continuum are given in some detail. The most pioneer forests are dominated by *Pinus banksiana* and *Quercus ellipsoidalis*. Slightly less pioneer stands are dominated by *Pinus resinosa* and *Pinus strobus*. Intermediate stands have *Pinus strobus* and some hardwoods such as *Quercus rubra* and *Acer rubrum*. In nearly climax stands, *Tsuga canadensis* is the main dominant, often with important amounts of *Betula lutea* or *Thuja occidentalis*. The most climax stands are dominated by *Acer saccharum* (and *Fagus grandifolia* in the extreme eastern part of the state), with *Ulmus americana*, *Tilia americana*, and *Ostrya virginiana* as associates. The characteristic herbs of these climax stands are the same as those found in the terminal forests of the upland continuum of southwestern Wisconsin.

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